1986

# Life History Variation In Artemisia Campestris On A Lake Huron Sand Dune System

Anne Felicite Stairs

# Life History Variation in *Artemisia campestris* on a Lake Huron Sand Dune System

by

Anne Felicite Stairs

Department of Plant Sciences

Submitted in partial fulfillment

of the requirements for the degree of

Doctor of Philosophy

Faculty of Graduate Studies

The University of Western Ontario

London, Ontario

April, 1986

ISBN 0-315-29466-3

THESIS ABSTRACT

A. F. Stairs

Life History Variation in *Artemisia campestris* on a Lake Huron Sand Dune System

Both monocarpic and polycarpic phenotypes occur in populations of *Artemisia campestris* growing on the sand dunes at Pinery Provincial Park, Ontario. Populations in three habitats differing in seral age, vegetation cover, vegetation type and proximity to the lake were selected for study. The distribution of phenotypes within and among populations, genetic control of the character and the relationship between number of reproductive events and age-specific survivorship were examined. Emergence patterns, fecundity, impact of herbivores, rosette diameter and growth patterns were also investigated.

Established plants within populations were mapped and tagged. Permanent plots were established to study seedling recruitment and to augment sample size. To determine if polycarpy was under genetic control, plants were grown under uniform conditions at two locations and a reciprocal transplant-replant experiment was performed.

The degree of polycarpy found was small and limited to one habitat, the heavily vegetated "transition zone". The ratio of juvenile to seedling survivorship was close to 1 in this habitat. Fecundity and emergence were both low, and plants were smaller at flowering than plants from other

habitats. On the dune ridge, the survivorship ratio was also close to 1. Emergence was low and fecundity intermediate. The plants on the dune ridge were larger, grew more rapidly and the critical rosette diameter for flowering was larger. Growth was also less affected by herbivores than in the other two habitats. Although repeated flowering was never observed, postflowering vegetative survival did occur. In the third habitat, the slack, mortality increased with age, and was higher than in the other habitats. Emergence was highly variable and fecundity was high.

Results from the uniform garden treatments suggest that plants from all habitats have the potential for polycarpy. Polycarpy was thought to be maintained by the indeterminate growth pattern of the species, by selection of individuals with low fecundity during the first flowering season that could flower again, and by gene flow among populations.

# ACKNOWLEDGEMENTS

I would like first to thank my supervisor, Dr. M. A. Maun, for his patience and encouragement over the years of this research, and for giving me the opportunity to learn in my own way. I would also like to thank the officials at Pinery Provincial Park, for allowing free access to the Park. The Province of Ontario and the National Sciences and Engineering Research Council greatly aided the research through financial support. Dr. Ian Thompson and my sister, Tracy Thomas, among others, provided much appreciated field assistance and company in the field. Ken Baldwin was not only my companion in the field and office, but guided me through the maze of computer software. Nick Panter, another willing field assistant, helped me clarify many thoughts in the initial planning stages of the project.

To Dr. Jane M. Bowles goes a very special thanks, for assistance in initial planning, assistance and companionship in the field, reading the thesis and doing the drawings and final figures for the thesis. Dr. Roger Green also deserves a special thanks for the hours he gave to (endless) discussions of the statistical analyses used, and for criticizing the thesis. Paul Threadgill, Dr. J. B. Phipps and Dr. D. Fahselt also provided useful comments on the thesis. Dr. Paul Handford mercilessly criticized the original research plan, and provided invaluable comments on the thesis itself, as he patiently read various drafts. He has also been an able intellectual model, and taught me much about the scientific paradigm.

Val Loewen's contribution to the completion of this thesis is immeasureable. She shared her love and understanding of nature, as well as her understanding of what it means to do a thesis, and without her love and support writing this thesis would have been much harder. Sarah, George and Judy Stairs never gave up their belief that I could and would finish.

My deepest gratitude goes to Dr. Paul Eric Smith, without whose constant and seemingly limitless capacity to listen and discuss this thesis would never have been completed. He also read and reread the thesis, and helped me wend my way through the mysteries of wordprocessing as painlessly as possible.

# TABLE OF CONTENTS

# LIST OF TABLES

# LIST OF FIGURES

# CHAPTER 1

# INTRODUCTION

## 1.1 Life history strategy

The life history characters of individuals within populations in part determine the spatial and temporal distribution of those populations. These characters include (among others) number of reproductive events, number of offspring produced per reproductive period, age to reproduction and age-specific survivorship. Much theoretical and empirical work has been addressed to these matters in the past two decades (see Stearns, 1976, 1980 and Dirzo and Sarukhan 1984 for reviews). In particular, efforts have been directed towards discovering whether sets of (coadapted) traits are associated with different sets of environmental conditions. These sets of (genetically determined) coadapted traits have been called "life history tactics" by Stearns (1976). They are also referred to as "life history strategies" by Harper and Ogden (1970), who reserved "tactics" for the phenotypic manifestation of the genetic strategy. However, as more data on life histories have been amassed, the whole concept of suites of coadapted life history characters has come into question, as natural systems are revealed to be far more complex than these theories predict. The differential sensitivity of traits to selection pressures (Ritland and Jain 1984),

pleiotropic effects (Dawson and Riddle 1983), developmental constraints (Law 1981) and lack of variability within populations in the characters (Heslop-Harrison 1965; Bradshaw 1984) may all lead to life history patterns which contradict predictions, or at best lead to theoretically suboptimal solutions (Stearns 1980). These arguments do not suggest that life history characters are never coadapted, nor that natural selection does not operate on life history characters in predictable ways. They do suggest that predictive models may have to be more complex, and that population biologists may have to look outside the field of demography to find explanations for life history phenomena, and indeed this is the current trend (King and Dawson 1983; Dirzo and Sarukhan 1984).

Some deterministic models, such as MacArthur and Wilson's (1967) r and K selection model, and Grime's (1977) Competition-Stress-Ruderal selection model, have other problems, such as defining the parameters on which selection is operating (Hairston, Wilbur and Tinkle 1979; Pianka 1970; Stearns 1976). The determinination of important environmental variables is fraught with difficulties in models which attempt to find correlations between habitats and suites of life history traits. Individuals of different ages and sizes may interact with the environment differently from one another and from what we may expect. One solution (Wilbur 1976) has been to use annual mortality rates as a measure of environmental uncertainty from the plant's "point of view".

In this thesis, an attempt is made to predict the occurrence of one life history character, the number of reproductive events, in relation to age-specific mortality rates. Other life history variables (seed number, age

to reproduction) were simultaneously examined in an attempt to discover pattern, but these were not included in the predictive model.

## 1.2 Monocarpy and polycarpy

A life history with multiple reproductive events is referred to as iteroparity or polycarpy in this study. One involving a single reproductive event followed by death is called semelparity or monocarpy. Annuality refers to a monocarpic life history completed within a year. Perennial monocarpy refers to a monocarpic life history that exceeds a year. This subsumes the term "biennniality", as most (though not all) biennials are facultative biennials, often taking longer than two years to complete the life cycle (Harper 1977; Kelly 1985b). "Perenniality" has often been used to refer to both longevity and polycarpy. This dual usage has been retained in this thesis only insofar as it is present in the literature, as in the models which follow.

The study of variation in the number of reproductive periods was instigated by Lamont Cole's (1954) challenging assertion that the intrinsic rate of increase of a perennial organism could be equalled by an annual through the addition of one offspring to its litter size (*sensu* Cole). Formally, this was stated as follows:

$$B_A = B_P + 1$$

where $B_A$ = fecundity of an annual and $B_P$ = fecundity of a perennial. This raised the question of why more species were not annuals, since the cost of surviving more than one year is intuitively greater than that of

producing one more offspring for most species. Attempts to contradict Cole's biologically unrealistic results produced a wave of more sophisticated models which modified the simplistic assumptions (no mortality, first year reproduction in perennials) of the original model. Murphy (1968) introduced years with no successful reproduction into the model and concluded that iteroparity would be favoured in habitats with variable reproductive success. Charnov and Schaffer (1973) predicted that age-specific mortality was the crucial variable in determining semelparity or iteroparity. Cole's model was changed (Charnov and Schaffer 1973) to

$$B_A = B_P + P/C$$

where P is postreproductive survivorship and C is juvenile survivorship. In environments where postreproductive survivorship is low relative to juvenile survivorship, semelparity should be favoured. Schaffer and Gadgil (1975) outlined these habitats as (1) harsh environments with high year to year variability; (2) environments with a high degree of disturbance and thus a high density-independent death rate and (3) transient habitats. Hastings and Caswell (1979), however, suggested that environmental variability has a multiplicative effect on fitness, not an additive one as proposed by Schaffer and Gadgil's model. Using a multiplicative model, they predicted that variability in juvenile mortality would lead to annuality if long-term expected growth rate was used as the fitness criterion, or that increased variability at any age would lead to perenniality, if the geometric mean of growth rate was used as the fitness criterion.

The above models concentrated on determining the optimality of annuality or perenniality under various conditions. The conditions under which monocarpic perennials would be selected for have only recently been evaluated. Monocarpic perennial populations share the disadvantage of a single reproductive event with annuals, and the disadvantage of delayed maturation with polycarpic perennials (Gross 1980). Schaffer and Gadgil (1975) suggested that biennniality would be favoured over annuality in environments where the growing season is short and fecundity is a sigmoidal function with a minimum limit of energy required and a maximum limit of the number of flowers that can be supported. Bell (1976) stated that, although in general early maturation maximises fitness, delayed reproduction may be favoured when fecundity increases with age and the juvenile class endures the highest mortality risk. Biennniality was not formally investigated until Hart (1977) modified Charnov and Shaffer's (1973) model. She substituted mortality in the first year of life ($C_1$) for the original juvenile survivorship term C, and survival after that stage ($C_2$) for post reproductive survival P. The set of models thus produced were as follows:

$$\lambda_A = C_1 S_A$$

$$\lambda_B = (C_1 C_2 S_B)^{1/2}$$

$$\lambda_P = C_2 + C_1 S_P$$

where $\lambda_A$, $\lambda_B$ and $\lambda_P$ are the intrinsic rates of increase of an annual, biennial and perennial population, $C_1$ and $C_2$ are defined as above, and S is fecundity. Since the critical variable remains age-specific mortality, the intent of the original model is unchanged. The modified model allows the

comparison of monocarpic perennial and polycarpic populations.

Hart (1977) agreed with earlier predictions that annuals should be found (though not necessarily favoured) in environments where $C_1$ was high relative to $C_2$, and perennials should be favoured when $C_2$ was high relative to $C_1$. She found no conditions under which biennials should be favoured. She predicted that they would be found in habitats with moderate survival values at both the seedling and postseedling stages. However, even in these habitats the annual or perennial life history would produce a higher rate of increase for equal fecundity.

Gross (1980) introduced a one year time lag to reproductive maturity for perennial and biennial populations into the model. The new model predicted that annuals and biennials would be equally disadvantaged in closed habitats because of low seedling recruitment. In open habitats, biennial and perennial life histories would be nearly equivalent. Including a more realistic pattern of increasing fecundity with age into the polycarpic life history, rather than assuming maximum reproduction during the first reproductive event, would give biennials the advantage in some field situations.

In Silvertown's (1983) site deterioration model, he suggested that the biennial and annual life histories are similar in intermittent habitats. He also pointed out the abundance of biennials in the Umbelliferae and Compositae. He suggested that the modular pattern of growth and the presence of a tap root in these families made delayed reproduction advantageous, since more time was allowed for accumulation of resources

for a single large reproductive event. Kelly (1985), in addition to developing the site deterioration model, suggested that biennials would be favoured over annuals when the survivorship of seeds in the soil is lower than vegetative plant survivorship, and when an extra year of growth produces an increase in the number of offspring produced. Thompson (1984) found that high resource allocation to reproduction, and high numbers of large seeds gave biennials an advantage over both annuals and perennials in closed habitats. Young (1981), in comparing perennial monocarpy with polycarpy, proposed a model in which a decrease in the ratio of prereproductive development time to time between reproductive episodes would favour perennial monocarpy.

1.3 Population differentiation and phenotypic plasticity

The above models implicitly assume that there is a genetically canalized optimal strategy for a given population in a specific environment. The problem is then one of determining whether annual monocarpy, perennial monocarpy or perennial polycarpy should be selected for in that habitat. Among conspecific plant populations, population differentiation may occur over very short distances (Jain and Bradshaw 1966; McNeilly 1968). Differentiation with respect to life history characters has also been found (Johnson and Cook 1968; Gadgil and Solbrig 1972; Snaydon and Davies 1972, 1976). In addition, there is evidence that genotypic differences in life history characters occur within a population (Law 1979). The implicit assumptions of optimal strategy models thus have some justification, but their generality may be limited.

The importance of phenotypic plasticity in morphological and physiological characters of plants has long been recognized (Bradshaw 1965, 1972). Bradshaw (1965) and Levins (1968) both predicted plasticity in rapidly (relative to generation time) fluctuating environments. Jain (1979) suggested that plasticity would be selected for in environments with a high degree of stochastic variation and no autocorrelation among years. In environments with regular long cycles of good and bad years and high seed longevity in the soil, polymorphism would be favoured. Caswell (1983) suggested that phenotypic plasticity in life history traits is a pervasive phenomenon which has not yet been entered into "genetically naive" life history theory. From his model, he predicted that plasticity in development rate is adaptive if the reproductive value increases from one stage to the next.

Caswell (1983) cautioned that "distinguishing adaptive variation from the unavoidable influence of the environment will not be easy". Smith-Gill (1983) distinguished two types of developmental plasticity. Developmental conversion occurs when an organism is genetically adapted to use specific environmental cues to dictate developmental events. It may operate through an on/off switch (arrested development) or by the production of alternate phenotypes, which may be abiotically controlled (another on/off switch) or maternally affected. The second type of plasticity, phenotypic modulation, is a passive response to the environment and may be nonadaptive, though selection may act to modify the results of modulation.

The evidence for genetic control of monocarpy and polycarpy in plant populations is scant. Hawthorn and Cavers (1976) note that weakened competitive stress induced weak polycarpy in *Plantago major*. Sterk (1975)

found weak polycarpy in populations of *Anthyllis vulneraria* on a sand dune system, but no genetic evidence was available. Floras contain many species identified as "annual or sometimes perennial" but the genetic system is unspecified.

1.4 Objectives of the study

*Artemisia campestris* has both monocarpic and polycarpic phenotypes growing in several habitats on the sand dune system along the eastern shores of Lake Huron. The proportion of each phenotype was unknown, but both phenotypes appeared sufficiently abundant to justify the taxon's use as a study organism. The first objective of the study was to determine the proportion of each phenotype by following the fates of individuals in the field. The second objective, determining the genetic control over the expression of monocarpy and polycarpy, was tested in reciprocal transplant-replant and uniform garden experiments.

The third objective was to determine the relationship between age-specific survivorship and the number of reproductive events. Populations from four habitats differing in seral age, vegetation cover, type of vegetation and proximity to the lake, were selected. It was predicted on the basis of the above models that in habitats with high mortality at all life stages monocarpy would be the dominant life history. In habitats with high juvenile (relative to adult) mortality, polycarpy would occur more frequently. Age to reproduction and fecundity were simultaneously examined, to determine possible patterns. Concomitant variables (measures of size and growth, effects of herbivores, density and seed mass) were included as

potential explanatory variables.

## 1.5 Thesis organization

Table 1.1 presents the plan of investigation, its relationship to the main variables studied and the chapters in which the study of these variables are located. Chapter 2 describes the taxonomy and morphology of *Artemisia campestris*. The study site, general sampling methods and reciprocal transplant-replant and uniform garden experiments are outlined in Chapter 3. Chapters 4, 5 and 6 describe the life history of the populations during the seedling, juvenile and reproductive phases respectively. Each chapter contains a brief review of the literature, description of methods pertaining only to that chapter, results and a discussion. To enable the reader to refer quickly to data from each chapter, a point summary is provided at the end of each results chapter.

Chapter 7 is a general discussion of the results as a whole. It addresses the objectives stated in the previous section and attempts to interpret the results in the light of life history theory.

## THESIS ORGANIZATION

| TOPICS | SUBTOPICS | WHERE FOUND | EXPLANATORY VARIABLES |
|---|---|---|---|
| Species | Taxonomy<br>Morphology | Chapter 2 | |
| Environment | Habitat description | Chapter 3<br>Appendix I | |
| Mortality Schedules | Seedling | Chapter 4 | Emergence patterns |
| | Juvenile | Chapter 5 | Size |
| | Reproductive | Chapter 6 | Damage |
| Life history characters | Duration of juvenile phase | Chapter 5 | Size |
| | Seed output | Chapter 6 | Damage |
| | Number of flowering seasons | Chapter 6 | Fertilization success |
| Differentiation or plasticity | Fate under uniform conditions | Chapter 5<br>Chapter 6 | Flowering schedules |

Table 1.1 Thesis organization, showing the main topics discussed in the thesis and subtopics (including main variables), where they are located in the thesis and possible explanatory variables included in the study.

# CHAPTER 2

# TAXONOMY AND MORPHOLOGY

## 2.1 Taxonomy

*Artemisia campestris* L. (Compositae: tribe Anthemidae), originally monographed in 1923 by Hall and Clements, has been described as a complex species composed of many races (Gleason and Cronquist 1963). Hall and Clements recognized six subspecies, differing in longevity, flower number, and the nature and amount of pubescence. Five out of the six subspecies are described as perennial and one (*A. campestris* ssp. *caudata* (Michx.) Hall and Clements) as biennial. Gleason and Cronquist (1963) recognized three phases in the northeastern flora, but gave a subspecific name to ssp. *caudata* only. Scoggan (1979) recognized five subspecies in the Canadian flora, including ssp. *caudata*. The taxon growing at Pinery Provincial Park can be identified, following these treatments, as *A. campestris* ssp. *caudata*, a mostly single-stemmed biennial or short-lived herbaceous perennial growing up to 1 m tall from a taproot, occurring on dunes and other sandy places. In the literature the taxon is often referred to as *A. caudata* (Hicks 1938; Bowles 1980; Baldwin 1982). Scoggan (1979) lists *A. caudata* as one of many synonyms of the subspecies *caudata*. Hereafter the subspecific name *caudata* will be understood, and the taxon will be referred to as *A. campestris*.

Confusion in the taxonomy of the species may be ascribed to the high degree of morphological variation in natural populations, even within a single subspecies. Hicks (1938) found variation in height, colour, pubescence, succulence, leaf form, root system and flowering pattern within *A. caudata* on an Indiana sand dune system. Although some variation could be attributed to varying levels of available nitrogen and light between habitats, she noted local variations even in adjacent plants, particularly in leaf form and amount of pubescence.

2.2 Distribution

The genus *Artemisia* comprises over four hundred species of perennial herbs and shrubs distributed throughout Europe, Asia, North America and South Africa. Members of the genus are dominant in the steppe communities of Asia, sagebrush communities of North America and the Karoo scrub of South Africa (Heywood and Humphries 1977). An Asiatic origin has been suggested for *A. campestris*. Its present distribution in North America is circumboreal, extending south to Florida and Arizona (Gleason and Cronquist 1963) but excluding desert areas (Hall and Clements 1923). In Canada, *A. campestris* occurs in all provinces and territories except Prince Edward Island, and as far north as the Arctic Circle (Scoggan 1979). The species occupies open places, often in sandy soils.

The subspecies *caudata* is also widely distributed, though concentrated in the eastern and central United States (Hall and Clements 1923) and southern Canada (Scoggan 1979). It occurs mainly on sand dunes, sandy beaches and other sandy places (e.g. river banks) along coasts, on shorelines

surrounding the Great Lakes and irregularly inland (Gleason and Cronquist 1963).

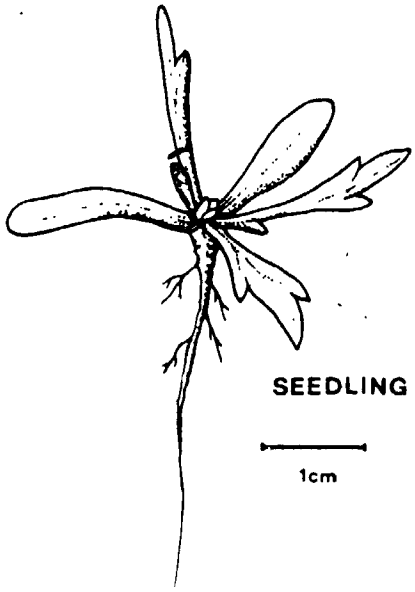
2.3 Phenology and morphology

Seedlings germinate throughout the summer season from May to October. True leaves appear within two weeks of the emergence of a seedling and a small rosette (more than two true leaves) is formed within a month. The rosette consists of entire leaves (Figure 2.1) which may become more or less divided according to habitat, season and age of the plant. The leaves themselves are grey-green in colour and more or less pubescent. A single stem is common in first year plants; after that multiple stems may appear.

Bolting, the elongation of cells formed by the apical meristem following floral induction, occurs at the Pinery in June or July sometime after the first year. Bolting lasts for approximately a month at which point flower buds appear. Flowering stems range in height from 10 to 120cm, and are spike-like to panicle-like in appearance depending on the size of the plant. Cauline leaves as well as basal rosettes are either persistent or deciduous during flowering. Vegetative stems sometimes occur in conjunction with reproductive stems.

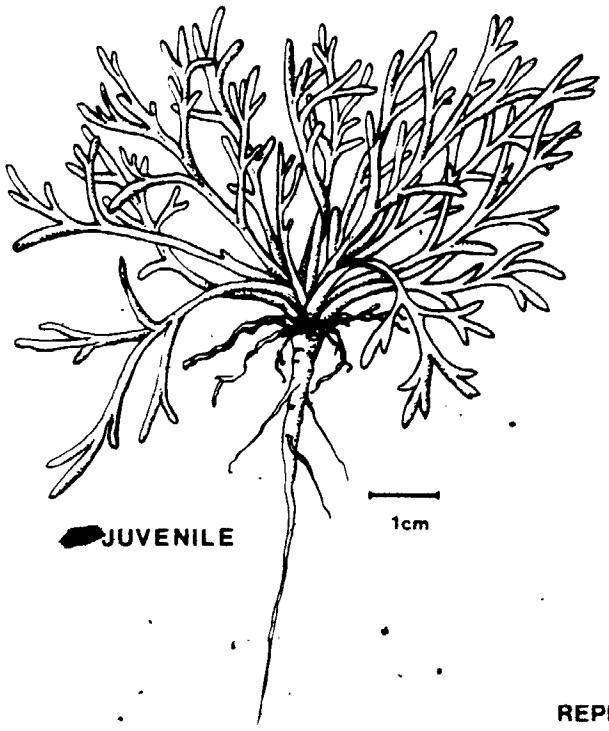
As in other Compositae, the total inflorescence comprises a number of flowering subunits, called involucres or capitula (Figure 2.1) which contain the individual flowers.There are generally 5-15 sterile disk flowers and 5-20 fertile ray flowers within a single capitulum (Gleason and Cronquist 1963). Individual capitula range from 2-5mm in length and the number per

Figure 2.1 The seedling, juvenile (rosette) and flowering phases of *Artemisia campestris*.



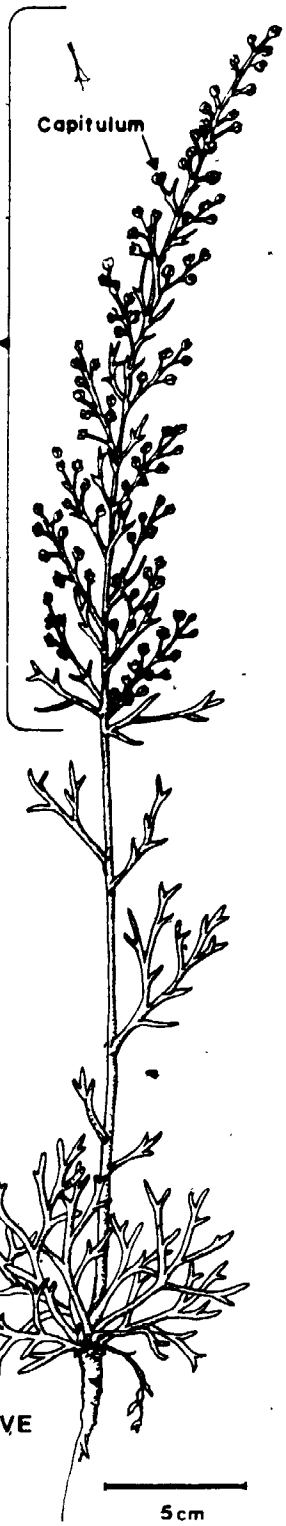
SEEDLING

1cm



JUVENILE

1cm




REPRODUCTIVE

5cm

plant varies greatly.

Anthesis takes place from early August to mid-September, though within an individual plant this stage is usually over within two or three weeks. Anther extrusion is followed by receptivity of the stigmatic surface. *A. campestris* is, like most of the genus, anemophilous and primarily outcrossing (Heywood and Humphries 1977).

After fertilization, the capitulum closes up until the seeds have ripened. The fruits are subcylindric cypselas, hereafter referred to as seeds, *sensu* Harper, Lovell and Moore (1970).Dispersal takes place from late fall through the winter. Unlike most other Compositae, members of the genus *Artemisia* do not possess a pappus. Seeds either fall near the parent plant or are dispersed short distances by wind. Germination on the parent plant, if the plant has fallen over, has also been observed.

Although the primary carbohydrate storage organ is the tap root, extensive lateral root systems particularly within the surface layers are developed also, and are assumed to provide anchorage for the plant as well as nutrients.

*A. campestris* is a hemicryptophyte, its aboveground parts dying back after exposure to prolonged periods of frost. At the Pinery this usually occurs in mid to late October, though plants in sheltered areas may grow through November. In plants which reach the flowering stage, mortality usually occurs after one reproductive period. However, two or even three flowering seasons are not unknown. In addition, some flowering plants

survive overwinter, remain vegetative during part of the following season but die before flowering again.

# CHAPTER 3

# STUDY AREA AND GENERAL SAMPLING TECHNIQUES

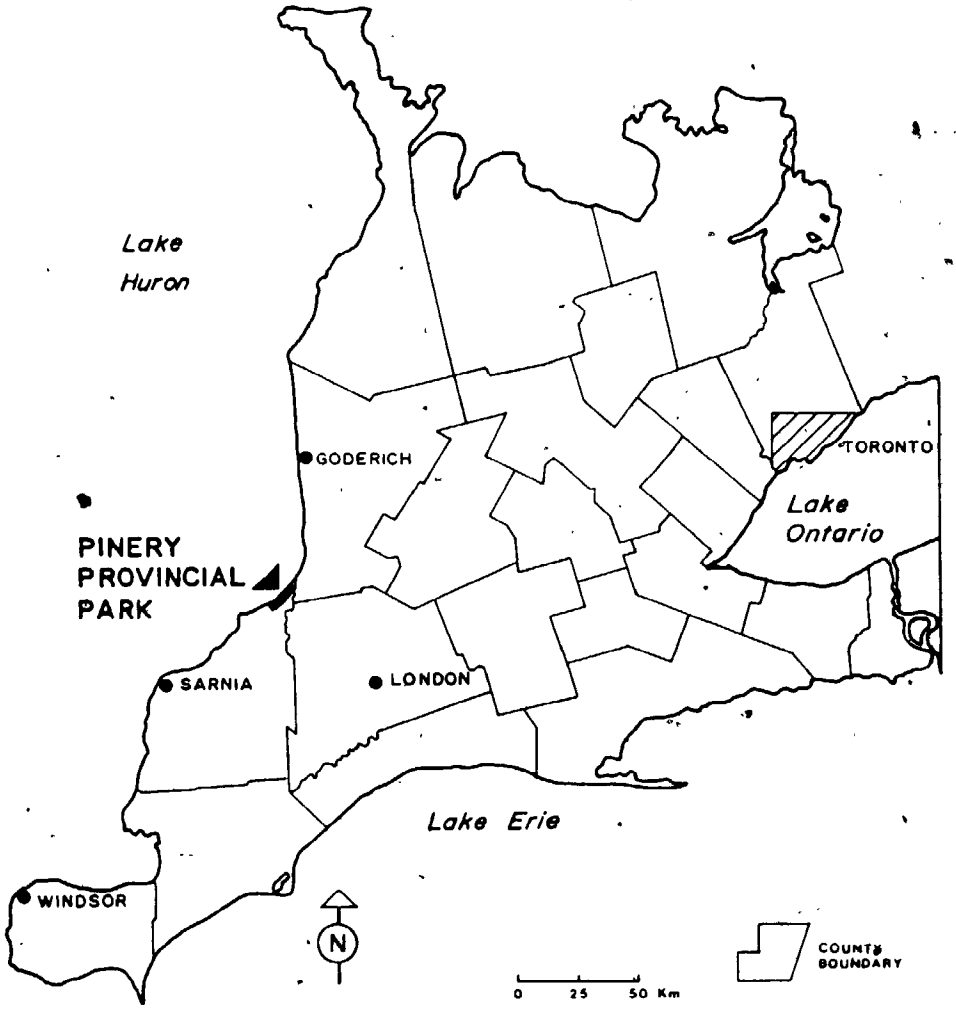
## 3.1 Pinery Provincial Park

The study was conducted at Pinery Provincial Park, which is located in Lambton County, Ontario on the southeast shore of Lake Huron (43° 15'N; 81°50'W; Figure 3.1). As part of the Georgian Bay-Lake Huron climatic area (Brown 1968 in Morrison and Yarranton 1974) it has a frost-free period of 150-160 days and mean monthly temperatures of 13-21° C in summer and -6-0°C in winter (Baldwin 1982). Precipitation averages 7-10cm per month. The driest months are February and March.

The most notable geomorphological features of the Park are the sand dunes, a series of dunes oriented obliquely to the shoreline. The youngest dunes (first and second dune ridges, nearest the shoreline) are transverse while the older ones are parabolic in shape (Bowles 1980). The dunes range in age from those in the process of forming to approximately 5000 years old (Morrison 1973).

The parent material of the dunes at the Park is sand eroded from bluffs north of Grand Bend. This is deposited on the beach by waves, and

Figure 3.1 Location of Pinery Provincial Park in southwestern Ontario.


Lake
Huron
GODERICH
PINERY
PROVINCIAL
PARK
SARNIA
LONDON
TORONTO
Lake
Ontario
Lake Erie
WINDSOR
N
0 25 50 Km
COUNTY
BOUNDARY

carried inland by wind. The sands give rise to soils classified in the Plainfield series of the Regosol Great Soils group, characterized by a weakly developed B horizon and little layering present in the young dunes (Morrison 1973). Olson (1958a) studied the development of dune soils on Lake Michigan and concluded that most pedogenesis occurs in the first 1000 years after stabilization. After that little improvement occurs and in fact deterioration may be evident.

Morrison (1973) classified the vegetation on the dunes into two groups. The first group, the colonizers or pioneer species, dominate the dune system on areas up to 1600 years old, increasing in diversity and abundance over that period. The second group, the persisting species, becomes evident on 800 year old dunes. They increase rapidly on 1600 year old dunes until they are completely dominant (except for gap areas) on dunes 2900 years and older. The vegetation on dunes between 800 and 2900 years old has been labelled "transition period" vegetation (Morrison 1973), a type occurring between full dominance by colonizers and complete takeover by persisting species. It is a vegetationally patchy area, with clumps of woody vegetation interspersed with grass-heathland. *Artemisia campestris* is a member of the colonizing group and occurs from the high beach into the grass-heathland patches of the transition zone.

### 3.2 The habitats

Four habitats of different ages within the pioneer stage were chosen on the basis of replicability of habitat type and abundance of the species. These were the high beach (0-50 years old), the first dune ridge (100 years),

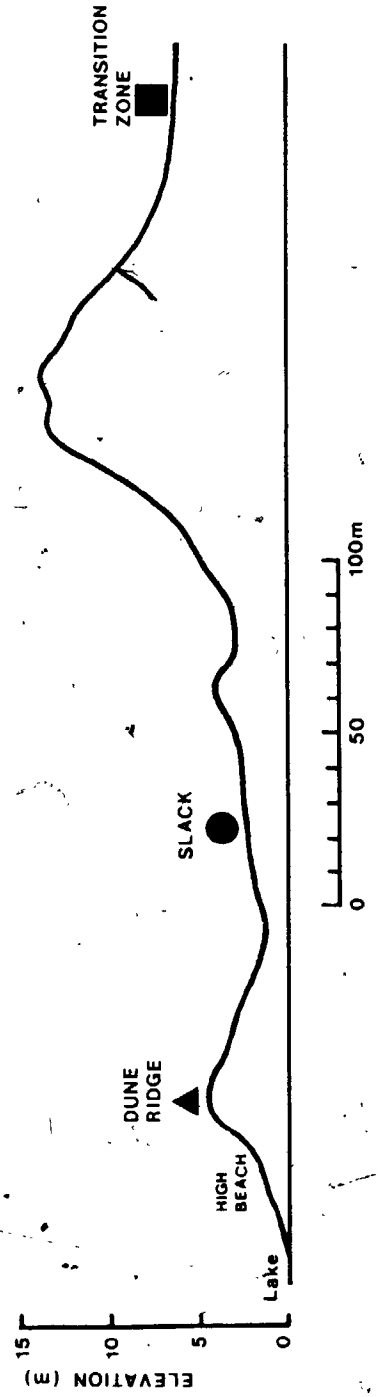
the slack (100-400 years) and the transition zone (800-2100 years) (Morrison and Yarranton 1974). Their relative position on a sand dune profile is illustrated in Figure 3.2.

The high beach lies closest to the lake and represents the earliest stage in the primary succession occurring at Pinery. It was defined as the area between the strand line (marked by storm-deposited gravel) and the first dune ridge. Vegetation is sparse and consists of *Artemisia campestris* L., *Cakile edentula* (Bigel.)Hook., *Ammophila breviligulata* Fern., *Calamovilfa longifolia* (Hook.)Scribn., *Populus balsamifera* L., *Oenothera biennis* L., *Salsola kali* L. and *Poa compressa* L.. The habitat is characterized by a constantly changing substrate subject to higher than average lake and wind levels during storms, particularly during the spring and fall. Sandslip at the base of the first dune ridge is another hazard to plant life.

The first dune ridge is located parallel to the shoreline and rises to approximately 5m above lake level. The slack or low occupies the area between the first and second dune ridges. The transition zone, corresponding approximately to Morrison's transition period vegetation, lies behind the second dune ridge.

Baldwin and Maun (1983) documented the microenvironmental and vegetational characteristics of the latter three habitats in detail (Table 3.1). The dune ridge and slack were characterized by low moisture content of soil surface (5-10cm) layers. The slack differed from the other habitats in having a higher percentage of coarse sand. Both the transition zone and the slack showed high daytime temperatures and large diurnal

Figure 3.2 Profile of sand dunes in the pioneer stage, showing the positions of the dune ridge, slack and transition zone habitats relative to the lake and lake level at Pinery Provincial Park.


TRANSITION ZONE
SLACK
DUNE RIDGE
HIGH BEACH
Lake
ELEVATION (m)
15
10
5
0
0
50
100m

| | HABITATS | | |
|---|---|---|---|
| | DUNE RIDGE | SLACK | TRANSITION ZONE |
| BARE AREA (%) | 44.0 | 58.1 | 4.9 |
| CHEMICAL COMPOSITION | | | |
| ORGANIC MATTER (%) | 0.4-2.0 | 0.4-2.0 | 4.5±1.5 |
| CALCIUM (ppm) | 530±137 | 2713±130 | 1558±328 |
| MAGNESIUM (ppm) | 32±29 | 34±3 | 75±16 |
| POTASSIUM (ppm) | 9±2 | 8±0 | 12±3 |
| PHOSPHORUS (ppm) | 2±1 | 2±1 | 2.0±0.5 |
| pH | 8.4±0.1 | 8.3±0.2 | 7.9±0.1 |
| AIR TEMPERATURE (C) | | | |
| SOIL SURFACE | 31.0 | 32.1 | 32.8 |
| 5 CM ABOVE SURFACE | 29.9 | 28.0 | 30.9 |
| SOIL TEMRERATURE (C) | | | |
| SOIL SURFACE | 34.5 | 35.4 | 32.4 |
| 5 CM BELOW SURFACE | 28.6 | 27.8 | 25.9 |
| SOIL MOISTURE (%) | | | |
| AT 5 CM DEPTH | 1.3 | 2.2 | 5.7 |
| AT 10 CM DEPTH | 2.7 | 2.9 | 4.2 |
| FIELD CAPACITY (%) | 10.7±0.9 | - | 12.8±1.8 |
| VAPOUR PRESSURE DEFICIT | | | |
| AT 50 CM ABOVE SOIL | 10.1 | 9.6 | 11.6 |
| WIND VELOCITY (km/hr) | | | |
| AT 50 CM ABOVE SOIL | 3.4 | 3.4 | 1.8 |
| BULK DENSITY | 1.6 | 1.6 | 1.4 |
| SOIL TEXTURE | | | |
| % BY WEIGHT | | | |
| FINE SAND (<0.25mm) | 55 | 39 | 57 |
| MEDIUM (<0.25-0.5mm) | 44 | 41 | 42 |
| COARSE (>0.5mm) | 1 | 20 | 1 |

Table 3.1 Physical and micrometeorological characters of the three sand dune habitats of different ages along a successional gradient along Lake Huron shoreline. (Data compiled from Baldwin and Maun 1983.)

fluctuations in temperature. Also characteristic of the transition zone were slightly higher air temperatures and a significant reduction in air turbulence above the soil surface (0.5-1m above ground). Transition zone soils showed a higher degree of organic matter and a higher moisture retaining capacity than the others. They also showed enhanced levels of $K^{+}$ and $Mg^{++}$ and depleted levels of $Ca^{++}$ in the surface layers.

In a sophisticated mathematical treatment of the differences between the three habitats, Baldwin (1982) showed clear separation between the open dune habitats (dune ridge and slack) and the more heavily vegetated transition zone. He considers the transition zone the youngest "stable" dune habitat. Because of the abundance of perennial vegetation relative to the other habitats the substrate itself is stabilized, allowing the accumulation of organic matter and true pedogenesis (Olson 1958a) to occur. Bowles (1980) looked at sand accretion and erosion in the young dune system near the coast. She found that sand movement was directly related to lack of vegetation, particularly in the slack. The slack appears to act as a wind corridor for winds off the lake. She proposes 55mm a year as an approximate mean change in sand level in unvegetated dunes. Partially vegetated areas show less change. Sand movement in the heavily vegetated transition zone is negligible except near paths and blowouts.

The vegetation of the first dune ridge and slack is sparse, dominated by *Calamovilfa longifolia*. Other species present are *Juniperus communis* L., *Populus balsamifera*, *Prunus pumila* L., *Andropogon scoparius* Michx. and *Artemisia campestris*. The bare sand surface accounts for about 44 and 58% of the area on the first dune ridge and slack respectively (Table 3.1).

Morrison and Yarranton (1974), based on the absence of significant correlations between species pairs, suggested that the vegetation was randomly distributed. The transition zone consists of diverse flora characteristic of the tall grass prairie complex of midwestern U.S. and Canada. Prominent among the species are *Andropogon scoparius*, *A. gerardii* Vitm., *Sorghastrum nutans* (L.)Nash., *Stipa spartea* Trin., *Artemisia campestris* and *Arctostaphylos uva-ursi* (L.)Spreng. (Baldwin and Maun 1983). Many other herbaceous and woody species as well as lichens and mosses occupy this habitat. The bare area is reduced to 5%. Apendix 1 contains detailed species lists for each habitat.

Although it is tempting to view the habitats as a successional series, this was not considered a useful approach to this study. There is no obvious directional change in vegetation (Kershaw 1973) in the younger habitats, particularly between the dune ridge and slack. Because of the high degree of disturbance inherent in young dune systems, co-occurring primary and secondary successions may invalidate the assumption that ecological conditions today model evolutionary processes in the past (Bowles 1980). Olson (1958a) suggested that dune systems, particularly in the young stages, should be viewed as a series of microsuccessions. Differences between the young habitats may be better viewed as habitat rather than seral age differences.

### 3.3 Site selection

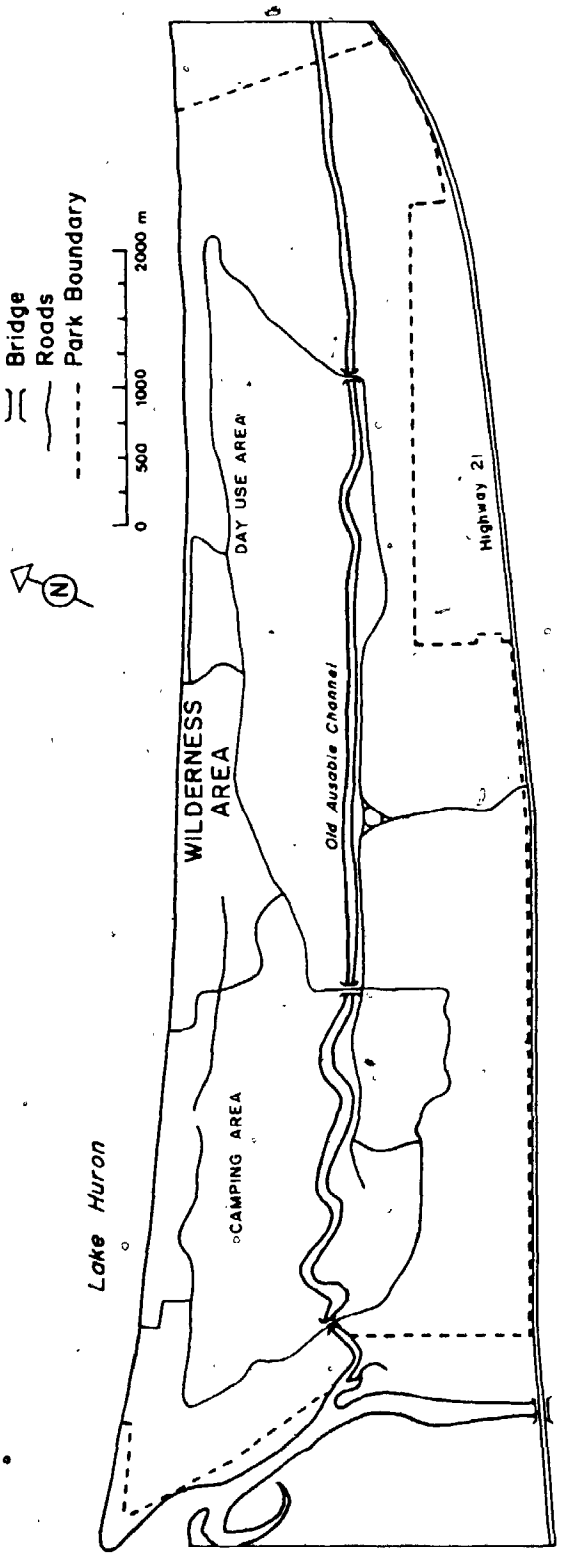
Since 1957 the Park has been a popular recreational area, heavily utilized by both day visitors and campers. For this reason the study was confined to a 1 km strip of land known as the Wilderness Area (Figure

3.3), accessible only by foot and therefore less disturbed by humans than the rest of the Park.

Five sites within each habitat type were selected in spring 1978. The objective of the mapping procedure was to allow relocation of marked plants and plots within each site, not to provide an accurate survey of the area. Therefore a method was chosen that provided sufficient accuracy to meet the objectives, but was logistically simple for one person to use after the initial location of sites and plants. In the continuous habitats (high beach and first dune ridge) an 875m strip of land was divided into 5 strips of equal length (175m) since no obvious natural demarcation points existed. Each strip was informally surveyed with compass and survey pole and subdivided into three 50m and one 25m length. These were marked with 12-inch wooden stakes. Some of these stakes were later vandalized; the strip was then resurveyed and the original stakes replaced with 18-inch stakes. On the dune ridge the sampled area comprised a 2.5m wide strip on either side of the central line to avoid obvious edge points. On the high beach a 5m strip shoreward of the line was sampled. Thus each site within these habitats was an area 5m x 175m.

In the slack, hummocks of sand and grass separating low flat areas provided natural divisions between sites. Five areas of varying sizes were chosen. These were laid out using crossed metal tapes and compasses to obtain approximate right angles. The corners of the rectangular areas were then marked with 12-inch stakes. A width of no less than 1m between the sampled area and surrounding boundary slopes or paths was excluded. Vandalized stakes were replaced (where possible) as explained above. The

Figure 3.3 Location of the Wilderness Area within Pinery Provincial Park.


Bridge
Roads
Park Boundary
0 500 1000 2000 m
N
DAY USE AREA
WILDERNESS AREA
Old Ausable Channel
Highway 21
CAMPING AREA
Lake Huron

dimensions of the areas surveyed were 50m x 20m, 20m x 10m, 50m x 20m, 35m x 15m and 30m x 20m.

In the transition zone sites were again clearly demarcated, in this case by shrub or small tree vegetation and/or older vegetated dunes. Care was taken that sites replicated one another as closely as possible in vegetation and vegetation patterns. No heavily disturbed areas were used. Surveying and staking proceeded as in the slack. The dimensions of the study areas were 15m x 6m, 14m x 7m, 14m x 8m, 13m x 5m and 15m x 6m.

In an ecological field study such as the one undertaken here the concept of locational replication deserves some attention. Some attempt to duplicate findings in more than one example of a habitat type is necessary in order to justify the generalization of a phenomenon (e.g. plant size) with only a low probability that its occurrence is the result of aberrant micro- or macro- environmental or historical events. In this study, attempts have been made to choose sites within a habitat type with a high degree of resemblance. Contiguous sites in the dune ridge and high beach should be more nearly alike (or at least show continuous distribution of ecological variables) than the sites separated by topographical or vegetational barriers. Within all habitat types, some sites are closer to campgrounds or picnic areas than others and the effect of human disturbance on populations of *A. campestris* varied among sites. Differential proximity to moving dunes is another unreplicable factor which particularly affects some slack and transition zone sites. Within the transition zone, age of the sites (judged by proximity to the lake) is another unduplicable factor. It should also be remembered that some habitats are inherently more variable than others.

Variability or unreplicability may be viewed as a habitat characteristic and not just sampling error.

Individual site descriptions with special reference to these differences are provided in Appendix I.

3.4 Population sampling

Each site was divided on paper into square metres and each point assigned latitudinal and longitudinal coordinates within the site, using one stake as a 0,0 point. The location of 60 established (not seedling) plants within each population was selected from a random numbers table. When no plant occurred at the random point, the nearest plant was chosen. Selected plants were tagged with aluminum tags attached loosely with nylon fishing line, which were then buried in the sand beside each plant to avoid vandalism. The exact location of each plant within the grid was recorded. Monitoring occurred approximately once a month during the growing season (May-October) through 1981. Survival, phenological stage, number of growing points, a measurement of size (rosette diameter if present, total height and height of inflorescence if reproductive) and evidence of disturbance, herbivory or other damage were recorded. Plants from this sample are referred to in the text as "tagged plants".

In September 1978, seedlings were similarly selected and tagged. The following spring it was noted that a large number of these individuals showed evidence of mortality due to the tagging method. These plants are thus not included in mortality estimates. Their use in other analyses is

noted when relevant.

In the spring of 1979, storms destroyed most of the high beach and the plants located there. In the following July, the beach was rendered unsuitable for further study by bulldozer action ordered by park officials in a "spring cleanup" program. Data from this habitat thus comprises only that collected in 1978 and up to July 1979, and reciprocal transplant data. The bulk of this thesis is based on data from the dune ridge, slack and transition zone.

In 1979 four 20cm x 50cm plots in each site were randomly selected for the investigation of seedling survival and growth. A plexiglass mapping table with a 10cm border on all sides was constructed with legs which fitted into metal tubes placed permanently in the ground. The table was engraved with a grid of square centimetres to avoid parallax. Acetate maps were overlaid on the grid and each seedling in the plot recorded every two weeks from June to September 1979. Mapping accuracy varied among habitats according to stability of the substrate which not only caused shifting of the poles but also shifting of the seedlings. Maximum displacement recorded was 1 cm over a two week period. In general seedling density was so low in this year that accuracy was not a significant problem. Corrosion of the plexiglass surface made the method unsuitable for long term study.

In 1980, the initial 20 x 50cm plots were nested in 1m x 1m plots and two additional plots per site were selected. All plots were marked with 18-inch wooden stakes at each corner, around which a metal quadrat was fitted. Two metre-sticks joined at right angles provided a simple and

convenient mapping device. Each plant within each plot was mapped on 10 to the square centimetre graph paper and assigned a number. Plots were monitored every two weeks for survival and recruitment during the 1980 and 1981 growing seasons. Every six weeks measurements concordant with those on the tagged plants described above were also recorded. Plants from these samples are referred to in the text as "plot plants".

Monitoring all plants during a given period required a minimum of six days. To minimize error due to time differences one replicate site of each habitat was monitored before proceeding to the next site within a habitat type. When recording dates are reported as a single date, this date refers to the date in the middle of the period.

3.5 Reciprocal transplant-replant and uniform garden experiments

The use of cloned material in uniform garden experiments provides a more representative sample of genotypes growing in field populations than seed-grown material (Quinn and Colosi 1977; Hume and Cavers 1981). Cuttings were grown through two "generations" in this project to rid the material of at least some maternal and environmentally induced variation.

Fifteen plants from each site (75 per habitat) were selected using coordinates chosen from a random numbers table and applied to the grids previously established for the main sampling (section 3.4). Collection took place on the mornings of June 23 and 24 1979. Each selected plant was cut just above the root and placed in damp paper towels inside a polyurethane bag which was then sealed, labelled and transported to the University of

Western Ontario greenhouse nursery as rapidly as possible. Rooting hormone was applied to the cut surface and the cutting placed in a sandy loam substrate on a bench in the nursery. The apical meristems were removed to induce multiple stem development. The nursery bench was misted every 3 minutes for 30 seconds. On October 15, 1979 each cutting, now rooted, was recut to provide at least 4 clones. Rooting hormone was applied to the new cuttings, which were then replanted on the bench and misted as above. The second generation cuttings were planted in 10cm plastic pots on March 10, 1980, filled with Pinery sand. The pots were placed randomly on benches in the greenhouse under a 16 hour light-8 hour dark regime. On May 28, 1980 plants from the high beach and transition zone were transplanted back to Pinery into their habitat of origin and their reciprocal habitat. Plants from all four habitats were transplanted to Labatt Field Station, London, Ontario, on May 29. All remaining cuttings in the greenhouse were repotted into 30cm earthenware pots and left in the greenhouse. All plants were watered manually every day (unless it rained) for the first two weeks after transplanting.

Only a small number of the original 75 cuttings per habitat survived to produce at least four surviving clones. The success rate was similar in plants from all habitats, between 17 and 20%. The survival rate immediately after transplanting was high in all environments.

Further sampling techniques specific to given projects are described in the appropriate chapters.

3.6 Analysis

Most of the statistical tests in this thesis were linear additive models which assume homogeneity of variances. This assumption was tested in each data set using the $F_{max}$ test (Sokal and Rohlf 1981). When significant heteroscedasticity was detected, Taylor's Power Law (Elliot 1977) was applied to determine the nature of the mean-variance relationship. Appropriate transformations, determined from this test, were applied. Transformations were limited to ones with simple biological interpretations (such as square root and $\log_e$) as long as these transformations fell within the confidence limits of the regression coefficient determined through Taylor's Power Law. When transformations were of no value in reducing heteroscedasticity, separate variance tests were utilized. Sokal and Rohlf (1981) were followed in choosing which comparison of means test was appropriate in each situation.

For much of the analyses, data from replicate populations were pooled within habitats. Replicates were analysed separately when variance in demographic parameters was thought to reflect closely the variance in the environment, as in the case of seedling emergence patterns. Increased access to statistical techniques not readily amenable to nested designs was thought to compensate for loss of information incurred by pooling replicates.

Unless otherwise stated, all analyses were performed using MINITAB Statistical Package (Ryan, Joiner and Ryan 1978) or the Biomedical Statistical Software Package (BMDP, Dixon 1983).

# CHAPTER 4

# EMERGENCE AND ESTABLISHMENT

## 4.1 Introduction

Germination, the extrusion of the radicle from the seed, is almost never directly observed in the field. Emergence from the soil is the first visible indication of a seed's viability. The number of seedlings emerged is thus the number germinating minus the number which die before emergence (Harper 1977). I have used the term emergence in this sense throughout this chapter. Harper (1977) has defined establishment as the next stage, when seedlings have expanded their own photosynthetic surface and are theoretically independent of seed reserves.

Growing evidence indicates that spatial and temporal patterns of emergence, and their interactions, strongly affect the establishment, growth (Chapter 5) and future reproductive success (Chapter 6) of plants. In species with two or more discrete emergence flushes, survival and fecundity often differ between cohorts, and are frequently negatively correlated (Arthur, Gale and Lawrence 1973; Howell 1981; Marks and Prince 1981). Growth rate is strongly affected by emergence rank within a cohort, with later emerging seedlings growing more slowly than early emergents (Ross and Harper 1972;

Weaver and Cavers 1979). The relative smaller size of late emergents may be evident up to three years after emergence (Cook 1980). Density of seedlings already emerged (Mead 1966; Ross and Harper 1972; Rabinowitz 1979; Mithen, Harper and Weiner 1984), patch type (Holt 1972; Werner 1977; Fenner 1978; Johnson and Thomas 1978; Thompson 1983; Hartgerink and Bazzaz 1984; Tremlett, Silvertown and Tucker 1984) and their interaction (Fowler 1984) affect plant establishment.

This chapter follows the fate of seedlings from emergence until the beginning of their second growing season. The following questions will be addressed:

1. Do seedlings emerge randomly in space and time within and between habitats?
2. Are there differences between and within habitats in overall seasonal emergence?
3. Does seedling mortality differ between habitats and years?
4. What are the effects of date of emergence, density and habitat on survivorship?
5. What is the relationship between seedling size and date of emergence, habitat and survivorship?

## 4.2. Materials and Methods

### 4.2.1. General methods

See Chapter 3 for details. Four permanent plots (50cm x 20cm) per site established in 1979 and six permanent plots (1m x 1m) per site established in 1980 were monitored at approximately two week intervals from May to October of 1979, 1980 and 1981. All emerging plants were recorded, mapped and assigned an identification number. Data from the 1979 season were used mainly for descriptive purposes as the small sample did not lend itself to statistical analyses.

Density of juvenile plants was determined from data collected within each plot at the beginning of May 1980 and 1981. Total population density was measured at the time of each seedling's emergence. Presence of other species within plots was recorded at the end of July 1981.

### 4.2.2. Emergence

Randomness of spatial distribution was tested in an attempt to quantify patchiness within and among habitats. Emergence data within plots summed across dates for each of 1980 and 1981 were fitted to the Poisson distribution using a $\chi^2$ test statistic. A significant $\chi^2$ indicates aggregation (Elliott 1977). The same data summed across plots within dates was examined to determine the statistical significance of observed emergence peaks.

To test differences in overall seasonal emergence, a two-level nested analysis of variance over sites within habitats for each year was performed

on transformed ($\log_e (x + 1)$) seedling number. One was added to allow taking the natural logarithm of 0-valued plots (Elliot 1977). A Minimum Significant Difference test modified for unequal sample sizes (Sokal and Rohlff 1981) was used to test differences between means. Differences between years within habitats were tested with a two-way ANOVA over sites within habitats and over years. When necessary, pairwise comparisons were made using separate variance t tests, with application of Bonferroni probabilities (Snedecor and Cochran 1980) to compensate for the multiple comparisons. Data were then pooled within habitats and a two-way ANOVA over habitats and years was performed using BMDP7D.

To explore the effects of population density, the presence of other species and differences between years, an analysis of covariance on seedling emergence between habitats was performed (BMDP1V). Covariates used were $\log_e (x + 1)$ density of vegetative plants of *A. campestris*, number of other species present and year. The analysis was followed by multiple regressions of seedling emergence on these variables within each habitat.

Three emergence cohorts were formed for each year by examining emergence peaks within each habitat in 1980 and 1981. Cohort 1 comprised those plants emerging during the spring peak, up to and including mid June 1980, and up to and including early June in 1981. Cohort 2 included seedlings emerging in late June, July and August of both years, periods of relatively low emergence. The September peak emergents constituted Cohort 3.

4.2.3 Seedling mortality

Product limit estimates (Kaplan and Meier 1958) of seedling survivorship within each habitat were computed using BMDP1L (Dixon 1983). Data were pooled over years. Seedlings still alive at the end of the study were treated as censored (Lawless 1982), as were seedlings in plots which were irrevocably lost through vandalism. The equality of survivorship curves between habitats was tested using both a generalized Savage statistic (Mantel 1966) and a generalized Wilcoxon statistic (Breslow 1970). Mean survival times, their standard errors and the 75th, 50th and 25th quantiles were computed. The 50th quantile is defined as the time at which 50 percent of the population was still alive, and is thus a measure of central tendency.

4.2.4. Seedling growth

Rosette diameter was used as a measure of growth (Werner 1975; Baskin and Baskin 1979a,b; Gross 1981; Gross and Werner 1983). Although not a measure of absolute growth since it does not take into account either the non-linear nature of growth or the growth of underground parts, it was thought useful for within species comparisons, and was logistically simple to measure in the field. Measurements were taken to the nearest half centimetre with a metre stick in mid-June, mid-August and late September 1980, and mid-June and late September 1981.

Difference in mean rosette diameter between habitats at the last September recording date in 1980 and 1981 was tested in an analysis of covariance (BMDP1V). The covariates initially selected were cohort, total

density at emergence, density of non-seedlings at emergence, number of species within the plot and year. Seedlings at the cotyledon stage were excluded from the analysis. Because of the high correlation between the density variables ($r_{180} = -0.86$) the analysis was repeated using the density variable with the highest t value for the regression coefficient. This was total density. The analysis of covariance was followed by a Student-Newman-Keuls comparison of means test for unequal sample sizes (Sokal and Rohlf 1969).

The analysis was repeated on rosette diameter measured in June 1981 for 1980 seedlings, including the rosette diameter obtained the previous fall as a covariate. Year was deleted as a variable. Seedlings at the cotyledon stage in September were assigned a value of 0.5cm. Only four seedlings survived overwinter in the slack. All of these were members of the second cohort. Because of the resulting singular variance-covariance matrix, equality of slopes within the full model could not be tested. After inspection the model was reduced to include only the number of species present and rosette diameter in the previous fall.

The effect of rosette diameter on probability of dying was estimated through a logistic regression (BMDPLR) of probability of dying on rosette diameter, habitat and cohort. In the logistic regression the probability of an event p (died, survived) was calculated from the data set. $\text{Log}_e (1 - p)/p$ was regressed on q where q is a linear function of the regressor variables (Walker and Duncan 1967; Bishop, Fienberg and Holland 1975; Dixon 1983). The analysis was performed in a forwards stepwise manner after evaluation of correlations between the independent variables. Because mortality factors

may be expected to differ between seasons, the effect on probability of dying overwinter and within the first year were estimated separately.

## 4.3 Results

### 4.3.1. Emergence

#### 4.3.1.1. Patterns of emergence in space and time

The detection of aggregation was strongly attached to the mean, both spatially and temporally. In many sites, low mean emergence was accompanied by a low variance due to the small number of large quadrats used. The lowest mean value at which spatial aggregation was detected was 1.67 seedlings per square meter (Table 4.1), but pattern was not consistently found in sites with means higher than this. The slack showed the most consistent association of mean with pattern detection, but this may be the result of having no intermediate mean emergence values for this habitat in this sample. Sites in the slack showed both the lowest ($0.33m^{-2}$) and the highest ($42.83m^{-2}$) mean emergence within plots summed over a whole season. Within-site variances were also highest in the slack, in 1981. Mean emergence within sites in the dune ridge ranged from $0.60m^{-2}$ to $9.20m^{-2}$. In the transition zone the range of emergence values was much narrower, from $0.50m^{-2}$ to $4.00m^{-2}$.

The coincidence of higher mean values with the detection of aggregation was also present in examining temporal patterns. The mean values necessary for consistent pattern detection appeared to be marginally

| | | | SPACE | | | TIME | | |
|---|---|---|---|---|---|---|---|---|
| HABITAT | YEAR | SITE | $\bar{x}$ | $s^2$ | SIGN. | $\bar{x}$ | $s^2$ | SIGN. |
| DUNE RIDGE | 1980 | 1 | 3.50 | 13.43 | *** | 4.67 | 26.67 | *** |
| | | 2 | 5.17 | 10.17 | NS | 3.88 | 8.98 | * |
| | | 3 | 1.67 | 7.07 | *** | 1.25 | 2.50 | NS |
| | | 4 | 1.17 | 1.37 | NS | 0.88 | 0.13 | NS |
| | | 5 | 9.20 | 152.70 | *** | 5.75 | 69.60 | *** |
| | 1981 | 1 | 1.17 | 1.37 | NS | 0.70 | 1.12 | NS |
| | | 2 | 1.50 | 1.50 | NS | 0.90 | 1.88 | * |
| | | 3 | 2.33 | 27.47 | *** | 1.40 | 2.04 | NS |
| | | 4 | 2.67 | 1.87 | NS | 1.30 | 2.01 | NS |
| | | 5 | 0.60 | 0.80 | NS | 0.30 | 0.46 | NS |
| SLACK | 1980 | 1 | 0.33 | 0.27 | NS | 0.25 | 0.21 | NS |
| | | 2 | 0.33 | 0.27 | NS | 0.25 | 0.21 | NS |
| | | 3 | 0.25 | 0.25 | NS | 0.13 | 0.13 | NS |
| | | 4 | 1.33 | 1.87 | NS | 1.00 | 1.71 | NS |
| | | 5 | 1.67 | 1.07 | NS | 1.25 | 3.07 | * |
| | 1981 | 1 | 6.50 | 183.10 | *** | 3.90 | 24.10 | *** |
| | | 2 | 42.83 | 2464.57 | *** | 25.70 | 3140.67 | *** |
| | | 3 | 18.25 | 974.92 | *** | 7.30 | 400.23 | *** |
| | | 4 | 0.33 | 0.67 | NS | 0.20 | 0.18 | NS |
| | | 5 | 20.67 | 1373.50 | *** | 12.40 | 278.93 | *** |
| TRANS-ITION ZONE | 1980 | 1 | 0.50 | 0.30 | NS | 0.38 | 0.55 | NS |
| | | 2 | 2.00 | 6.40 | ** | 1.50 | 3.14 | * |
| | | 3 | 2.67 | 2.67 | NS | 1.38 | 12.27 | *** |
| | | 4 | 4.00 | 17.60 | *** | 3.00 | 14.86 | *** |
| | | 5 | 4.33 | 14.27 | ** | 3.25 | 3.93 | NS |
| | 1981 | 1 | 3.17 | 3.77 | NS | 1.90 | 11.66 | *** |
| | | 2 | 1.50 | 2.30 | NS | 0.90 | 4.77 | *** |
| | | 3 | 2.50 | 21.90 | *** | 1.50 | 5.83 | *** |
| | | 4 | 2.50 | 2.70 | NS | 1.50 | 8.72 | *** |
| | | 5 | 2.50 | 0.70 | NS | 1.50 | 9.39 | *** |

Table 4.1 Aggregation of seedling emergence in space (among plots and over all observation dates) and time (within plots among observation dates). Shown are mean number of seedlings emerged per square metre ($\bar{x}$) and associated variances ($s^2$) in replicate sites within each habitat in 1980 and 1981. Significance levels: * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$; NS: nonsignificant.

higher in the dune ridge than in the other habitats. The slack had the highest and lowest mean values for seedling emergence per square metre for single observation dates. These ranged from $0.20m^{-2}$ per recording period to $25.70m^{-2}$. Variances in temporal distribution were also highest in the slack, the largest ones occurring in 1981. Seedlings emerging per observation date ranged from $0.30m^{-2}$ to $5.75m^{-2}$ in the dune ridge. In the transition zone, mean values ranged from $0.38m^{-2}$ to $3.25m^{-2}$.

Figures 4.1a and 4.1b show the emergence and rainfall patterns in all three habitats for both years. In the dune ridge, emergence occurred throughout the season in 1980, with peaks in the spring and fall. In 1981 overall emergence was less and dropped to 0 in midsummer. A similar pattern was seen in the transition zone but with stronger peaks in the fall of both years. In the slack, emergence was low throughout 1980, with no peaks evident at any time. In 1981, both spring and fall peaks were evident, with a very large emergence event accompanied by a very large variance occurring in early September. Emergence occurred throughout the 1981 season in the slack.

There appears to be a relationship, though not a simple one, between heavy rainfall in the fall and emergence. Rainfall was heaviest in late August-early September 1981, and this coincided with the highest emergence recorded in the study. In September 1980 there was also a long wet period, but this took place late in the month. Emergence was lower in this period than in the corresponding period in 1981. The spring 1980 emergence peak closely followed a period of heavy rain. Precipitation was sporadic and generally less throughout the middle of the season than in the fall and

Figure 4.1a Distribution of rainfall (cm) at Pinery Provincial Park from May through September 1980 (top). The lower figure shows the mean number of emerged seedlings $m^{-2}$, with 95% confidence limits derived from $\log_e (x + 1)$ transformed data, observed on different dates in 1980.

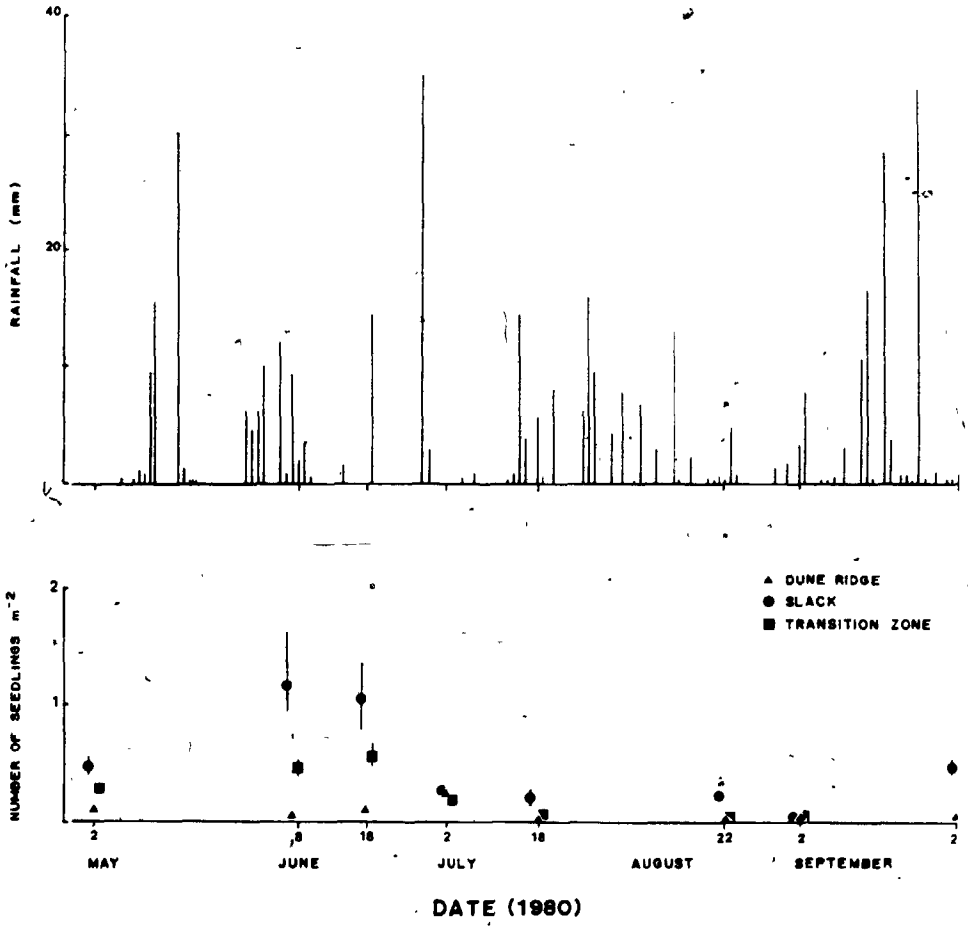
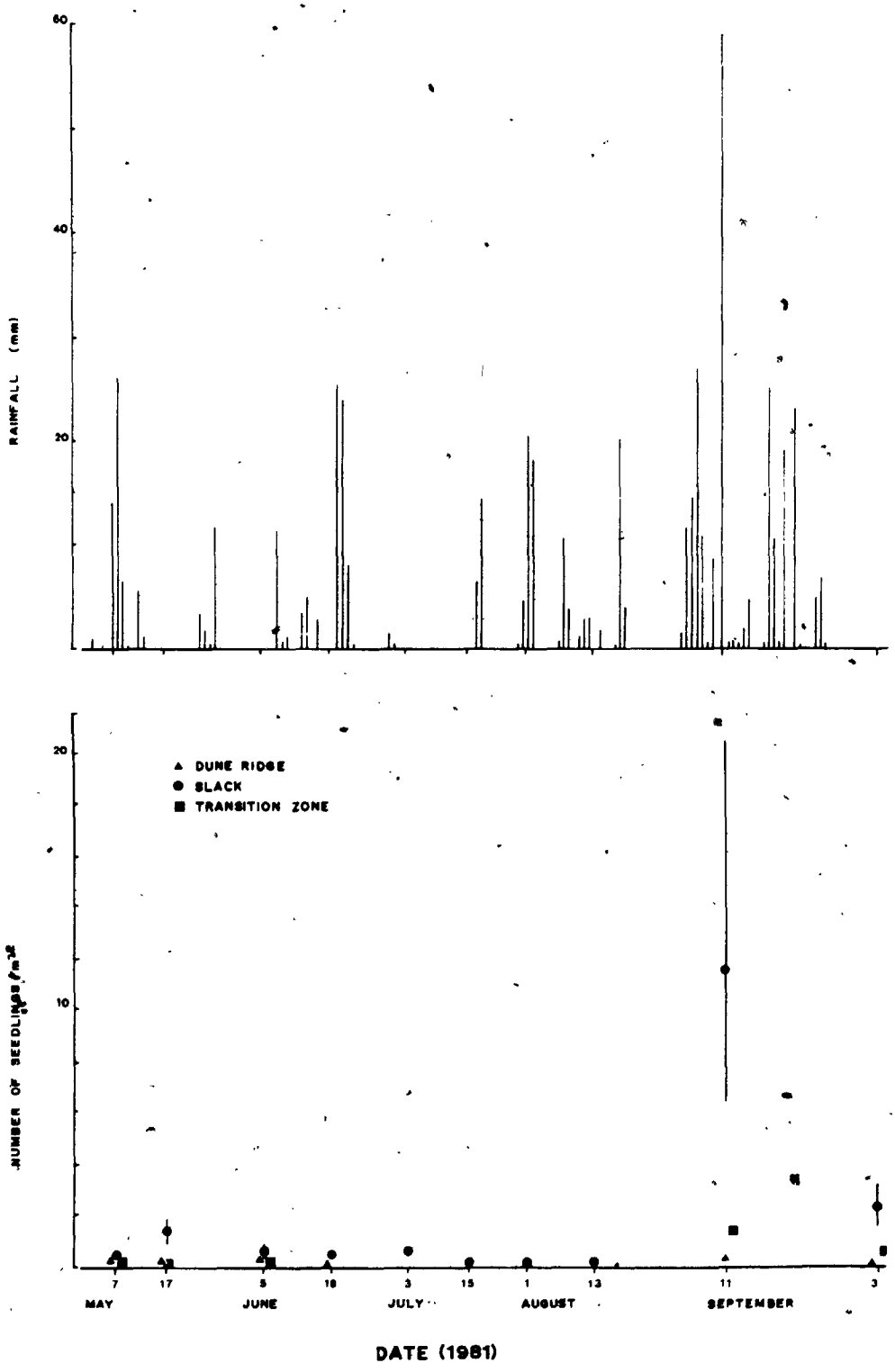

40
20
0
RAINFALL (mm)
2
1
NUMBER OF SEEDLINGS m⁻²
DUNE RIDGE
SLACK
TRANSITION ZONE
2
8
16
2
16
22
2
2
MAY
JUNE
JULY
AUGUST
SEPTEMBER
DATE (1980)

Figure 4.1b Distribution of rainfall at Rinery Provincial Park from May through September 1981 (top). The lower figure shows the mean number of emerged seedlings $m^{-2}$, with 95% confidence limits derived from $\log_e (x + 1)$ transformed data, observed on different dates in 1981. Note that due to the high number of seedlings in 1981, and the accompanying wide confidence intervals, there is a scale difference between Figure 4.1a and Figure 4.1b.


RAINFALL (mm)
60
40
20
NUMBER OF SEEDLINGS/m²
20
10
▲ DUNE RIDGE
● SLACK
■ TRANSITION ZONE
7
17
5
19
3
15
1
13
11
3
MAY
JUNE
JULY
AUGUST
SEPTEMBER
DATE (1981)

spring, and emergence followed the same pattern. Higher temperatures during this season may also affect emergence.

4.3.1.2. Overall seasonal emergence

The two-level nested ANOVA (Table 4.2) showed significant among site variation but no differences among habitats. Thus variance within habitats was significantly greater than variance among habitats. In 1980, one site (DR2) in the dune ridge had a significantly higher mean than two sites in the slack (SL1 and SL5) and one in the transition zone (TZ5). In 1981, one site in the slack (SL5) had a significantly higher mean than all other sites except two in the slack (SL2 and SL4) and one in the transition zone (TZ5). The reversal in the emergence hierarchy between years of sites SL5 and TZ5 suggests that emergence patterns cannot be explained solely by site differences in "favourability for emergence".

The analysis of variance within each habitat over years showed no differences in overall seasonal emergence among sites or years in the dune ridge and transition zone. Strong heteroscedasticity in the slack necessitated the use of a separate variance analysis of variance which showed significant differences ($F_{8,22} = 4.61$; $p = 0.002$) among site-year combinations. However, none of the pairwise comparisons were significant using separate variance t tests.

Figure 4.2 shows the mean number of emerged seedlings and 95% confidence limits around the mean, in all habitats in 1980 and 1981. The slack had the greatest range between years in overall seasonal emergence per

1980

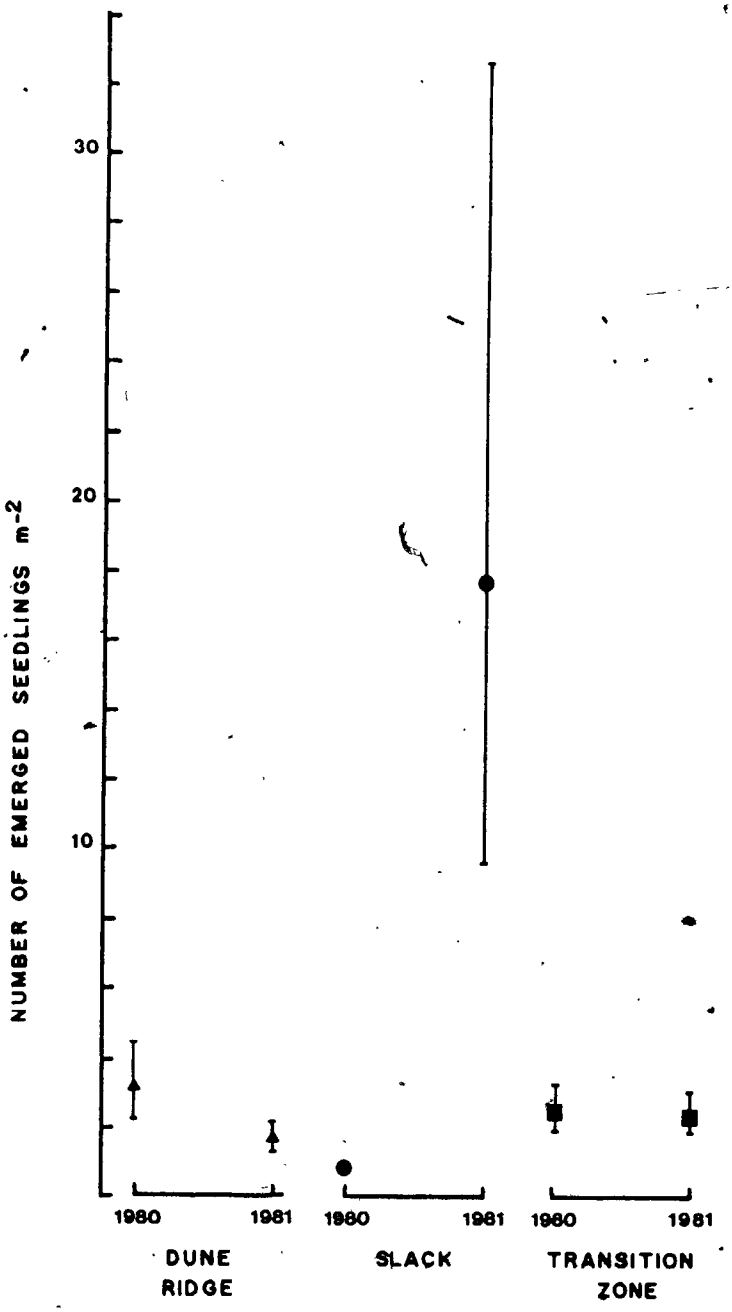
| SOURCE | DF | DF′ | SS | MS | MS′ | F | F′ |
|---|---|---|---|---|---|---|---|
| Among habitats | 2 | | 7.00 | 3.50 | | | 3.77 |
| Among sites | 13 | 12 | 11.53 | 0.89 | 0.93 | 2.00* | |
| Within sites | 71 | | 31.52 | 0.44 | | | |
| Total | 86 | | 50.04 | | | | |

1981

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Among habitats | 2 | | 12.38 | 6.19 | | | 2.11 |
| Among sites | 13 | 12 | 35.81 | 2.75 | 2.94 | 3.53*** | |
| Within sites | 71 | | 55.40 | 0.78 | | | |
| Total | 86 | | 103.59 | | | | |

Table 4.2 Two level nested analysis of variance (within sites within habitats) on $\log_e (x + 1)$ transformed seasonal emergence data in three habitats in 1980 and 1981. Satterthwaite's F approximation ($F'$) for unequal sample sizes is reported for among habitat variation (Sokal and Rohlf 1981). DF = degrees of freedom; SS = sums of squares; MS = mean squares. Significance: * $p \leq 0.05$; *** $p \leq 0.001$.

Figure 4.2 Overall seasonal emergence in three habitats in 1980 and 1981. True arithmetic means of number of seedlings per square metre are shown. 95% confidence limits were calculated from the variances of the $\log_e (x + 1)$ transformed data.


NUMBER OF EMERGED SEEDLINGS m-2
30
20
10
1980
1981
1980
1981
1980
1981
DUNE RIDGE
SLACK
TRANSITION ZONE

square metre. The 95% confidence limits accompanying the 1981 mean were very wide, even under a natural log transformation. Overall emergence was remarkably constant in the transition zone with means of $2.5m^{-2}$ and $2.4m^{-2}$ in 1980 and 1981 respectively.

In testing the equality of means over habitats and years a separate variance analysis of variance had to be employed. This was significant ($F_{5,92}$ = 4.31; $p < 0.001$). Separate variance t tests showed significant differences between the slack in 1980 and all other habitat-year combinations except the dune ridge in 1981.

4.3.1.3. Population density and presence of other species

The analysis of covariance of year, number of other species and density of juvenile conspecifics with seedling emergence indicated significant differences in slope among habitats ($F_{6,162} = 5.94$; $p<0.001$). The main analysis was therefore terminated.

Results of the regressions of seedling emergence on juvenile density, year and number of other species within habitats are presented in Table 4.3. The accompanying analyses of variance are reported in Table 4.4. In the dune ridge, the total regression was not significant. In the slack the regression was highly significant though the total regression accounted for only 31% of the variation within the sample. Of the explained variation 72% of the information was incorporated in the year variable and 24% in the number of other species present. In the transition zone, the regression was again significant, though only 9% of the total sample variance was

DUNE RIDGE

| REGRESSOR | b | S.E. | t | SIGN. |
|---|---|---|---|---|
| INTERCEPT | 0.82 | 0.46 | 1.78 | NS |
| LOGEJUV | 0.12 | 0.11 | 1.07 | NS |
| YEAR | -0.32 | 0.21 | -1.55 | NS |
| NSPECIES | 0.13 | 0.10 | 1.28 | NS |

SLACK

| REGRESSOR | b | S.E. | t | SIGN. |
|---|---|---|---|---|
| INTERCEPT | -2.02 | 0.66 | -3.35 | * |
| LOGEJUV | 0.16 | 0.20 | 0.77 | NS |
| YEAR | 1.25 | 0.30 | 4.14 | *** |
| NSPECIES | 0.46 | 0.18 | 2.58 | * |

TRANSITION ZONE

| REGRESSOR | b | S.E. | t | SIGN. |
|---|---|---|---|---|
| INTERCEPT | -9.02 | 0.47 | -0.04 | NS |
| LOGEJUV | 0.33 | 0.12 | 2.69 | * |
| YEAR | 0.10 | 0.16 | 0.64 | NS |
| NSPECIES | 0.05 | 0.05 | 1.08 | NS |

Table 4.3 Regression coefficients (b), standard errors (S.E.) and t statistics from the regression of $\log_e (x+1)$ seedling emergence on $\log_e (x+1)$ density of juvenile conspecifics (called LOGEJUV), year and number of other species present within each of three habitats. Significance: * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$; NS not significant.

DUNE RIDGE

| SOURCE | D.F. | S.S. | M.S. | F | SIGN. |
|---|---|---|---|---|---|
| REGR. | 3 | 3.33 | 1.11 | 1.81 | NS |
| RES. | 54 | 33.10 | 0.61 | | |
| TOTAL | 57 | 36.44 | | | |

SLACK

| SOURCE | D.F. | S.S. | M.S. | F | SIGN. |
|---|---|---|---|---|---|
| REGR. | 3 | 32.97 | 10.99 | 9.26 | *** |
| RES. | 52 | 61.73 | 1.89 | | |
| TOTAL | 55 | 94.70 | | | |

TRANSITION ZONE

| SOURCE | D.F. | S.S. | M.S. | F | SIGN. |
|---|---|---|---|---|---|
| REGR. | 3 | 3.34 | 1.11 | 2.83 | * |
| RES. | 56 | 22.08 | 0.39 | | |
| TOTAL | 59 | 25.42 | | | |

Table 4.4 Analyses of variance from the regression (REGR.) of $\log_e (x+1)$ seedling emergence on $\log_e (x+1)$ density of juvenile conspecifics, year and number of other species present within each of three habitats. Significance: * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$; NS not significant.

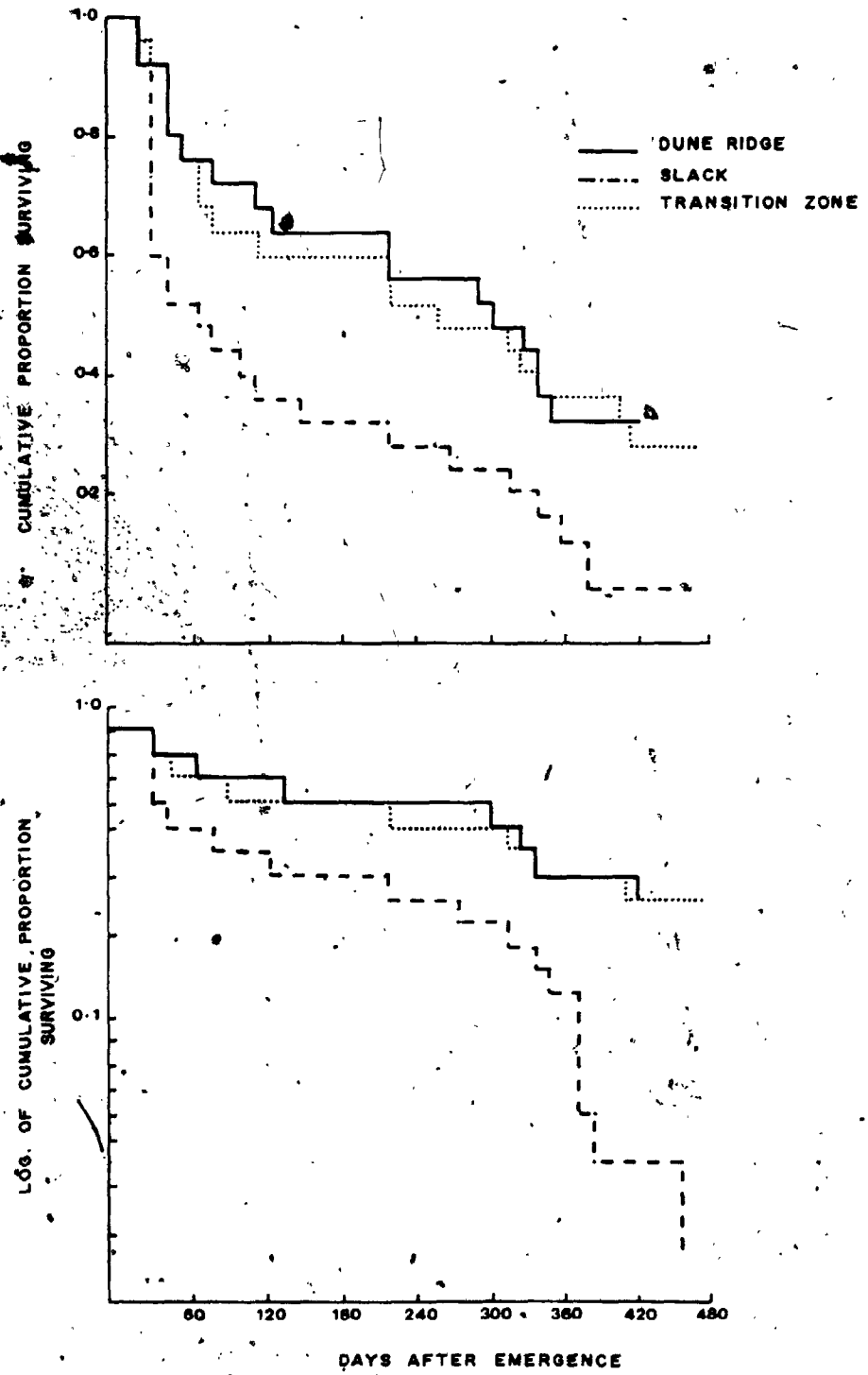
explained. Density of conspecifics was the only significant coefficient, accounting for 82% of the information (Table 4.3).

4.3.2. Seedling mortality

The cumulative proportion surviving within each habitat and the logarithm (mortality rate) of this are shown in Figure 4.3. Mean survival times, their standard errors and the 75th, 50th and 25th quantiles (where calculated) are reported in Table 4.5. The mean survival time for seedlings in all habitats was less than a year, approximately nine months in the dune ridge and transition zone and half that in the slack. However, seedling survivorship is not normally distributed since most seedlings that die do so soon after emergence. Therefore the 50th quantile is a better estimate of central tendency in the distribution. Fifty per cent of seedlings were dead after ten months in the dune ridge, eight months in the transition zone and after less than two months in the slack. The logarithmic plot (Figure 4.3, lower) indicates that the rate of mortality was greater in the slack than in the other habitats after the first month and also after the first year of life.

Kaplan-Meier survival estimates until the following season were 0.49, 0.27 and 0.48 for the dune ridge, slack and transition zone respectively. The generalized Wilcoxon and generalized Savage statistics, testing differences in survivorship among habitats, were both highly significant ($p < 0.001$).

Figure 4.3 The cumulative proportion surviving, and log of the cumulative proportion surviving, of the seedling population emerging in the dune ridge, slack and transition zone in 1980 and 1981 (data pooled over years).


1·0
0·8
0·6
0·4
0·2
CUMULATIVE PROPORTION SURVIVING
DUNE RIDGE
SLACK
TRANSITION ZONE
1·0
0·1
LOG. OF CUMULATIVE PROPORTION SURVIVING
60
120
180
240
300
360
420
480
DAYS AFTER EMERGENCE

| | DUNE RIDGE | SLACK | TRANSITION ZONE |
|---|---|---|---|
| Mean survival time (days) | 276.37 | 137.16 | 261.86 |
| S.E. | 41.69 | 14.79 | 47.69 |
| 75th Quantile (days) | 63 | 21 | 42 |
| 50th Quantile | 303 | 56 | 248 |
| 25th Quantile | | 277 | |

Table 4.5 Mean survival time in days, standard errors and 75th, 50th and 25th quantiles for seedling survivorship in the dune ridge, slack and transition zone habitats.

### 4.3.3. Growth of seedlings

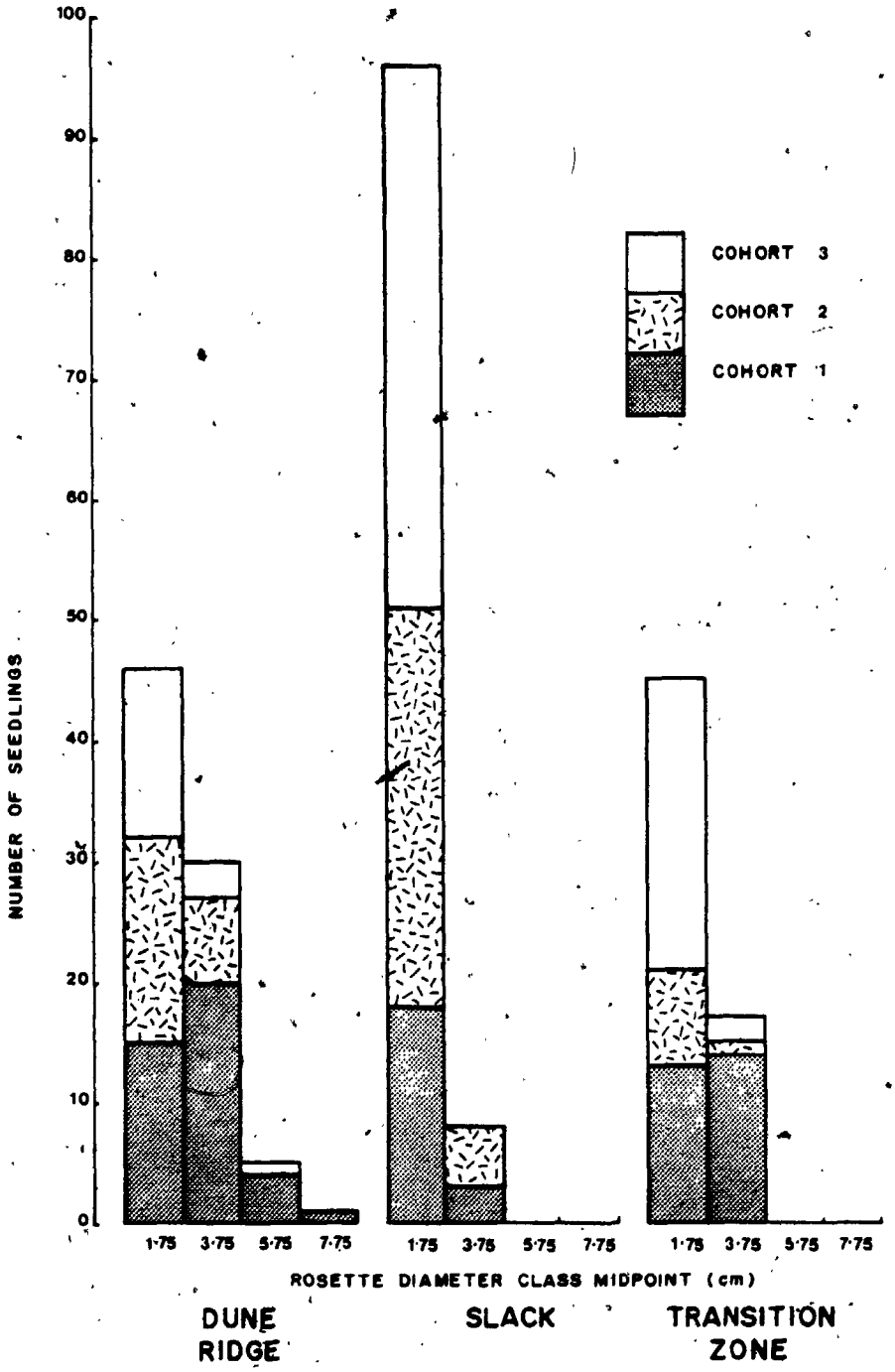
#### 4.3.3.1. Mean rosette diameter at the end of the first growing season

Size distributions by habitat for each cohort in the September following emergence are shown in Figure 4.4. All distributions except Cohort 1 in the dune ridge and transition zone and Cohort 3 in the slack are strongly skewed, showing many more seedlings in the smallest size class than in the larger ones. Cohort 3 in the slack is only represented in the first size class. Cohort 1 in the transition zone is evenly distributed between the two smallest size classes. On the dune ridge, Cohort 1 has a wider range than in the other habitats. The modal size class in the dune ridge is also larger than in the other habitats and cohorts.

Table 4.6 contains raw means and standard errors, and means adjusted for cohort and plot density effects, of fall rosette diameter. The assumption of equality of slopes between habitats in the analysis of covariance was justified ($F_{8,167} = 0.74$; $p = 0.65$). Significant differences were found between the adjusted group means ($F_{2,175} = 5.78$; $p < 0.01$). The comparison of means test showed significant differences at the 0.05 level between the dune ridge and both the slack and transition zone.

The regression of the covariates on rosette diameter was significant ($F_{4,175} = 5.79$; $p < 0.001$). The covariate cohort was highly significant ($b = -0.56$; $t_{177} = -4.44$; $p < 0.001$), as well as total density ($b = -0.21$; $t_{177} = -2.12$; $p < 0.05$). The number of species present and year were both non-significant. Thus later cohorts were smaller in size than earlier ones, and plants in

Figure 4.4 Frequency distributions of rosette diameter (in centimetres) in September 1980 and 1981 for seedlings which emerged that summer. Distributions are shown by habitat and cohort. Cohort 1 emerged in the early season (approximately up to mid-June); Cohort 2 emerged in mid-season; and Cohort 3 emerged in September. Measurements for Cohort 3 are for the September following emergence.


100
90
80
70
60
50
40
30
20
10
0
NUMBER OF SEEDLINGS
COHORT 3
COHORT 2
COHORT 1
1·75
3·75
5·75
7·75
ROSETTE DIAMETER CLASS MIDPOINT (cm)
DUNE RIDGE
SLACK
TRANSITION ZONE

SEPTEMBER 1980 and 1981

| HABITAT | n | $\bar{X}$(cm) ± S.E. | ADJUSTED $\bar{X}$ |
|---|---|---|---|
| DUNE RIDGE | 78 | 2.73 ± 0.18 | 2.76 |
| SLACK | 48 | 1.89 ± 0.21 | 1.96 |
| TRANSITION ZONE | 56 | 2.08 ± .028 | 1.97 |

JUNE 1981

| | | | |
|---|---|---|---|
| DUNE RIDGE | 33 | 4.45 ± 0.54 | 4.90 |
| SLACK | 4 | 6.50 ± 1.13 | 7.11 |
| TRANSITION ZONE | 34 | 4.96 ± 0.56 | 4.45 |

Table 4.6 Means ($\bar{X}$), adjusted means and standard errors (S.E.) of rosette diameter from the analyses of covariance including cohort, density, species and year (in the September analysis) as covariates.

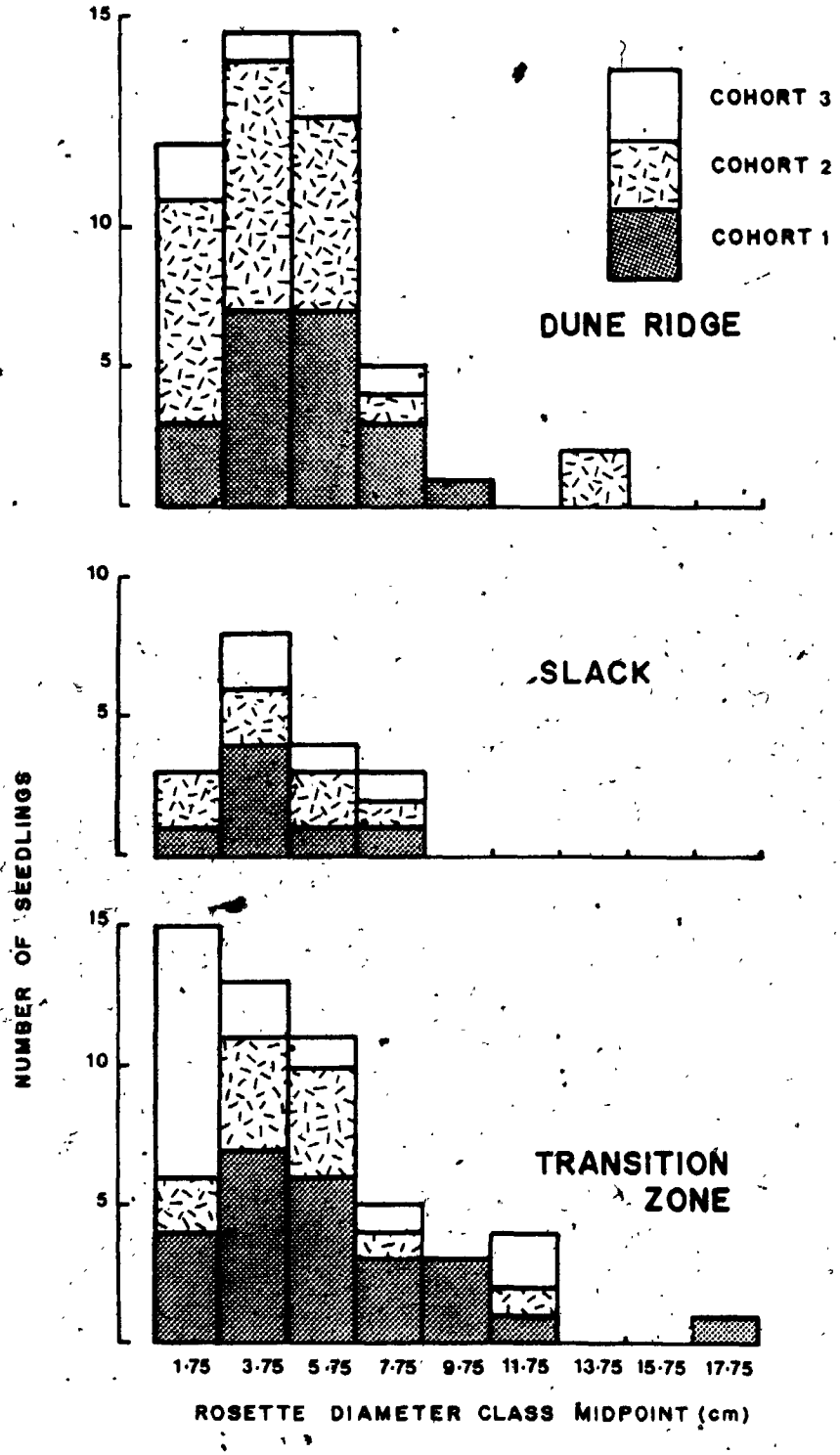
high density plots at emergence were smaller than those in lower density plots.

4.3.3.2. Rosette diameter at the beginning of the second growing season

Rosette diameter distributions in June 1980 and 1981 for seedlings emerging the previous year are shown in Figure 4.5. Distributions for all habitats were less strongly skewed than the previous fall (Figure 4.4) except Cohort 3 in the transition zone. The range is greatest in the transition zone, because of one particularly large individual, and smallest in the slack. The depleted sample size in the slack may have affected this. In general, except in the transition zone, cohort differences were not remarkable by the beginning of the second season.

The full model testing the difference in mean rosette diameter in June 1981 could not be evaluated statistically because no test was available for the equality of slopes (section 4.2.3). Heuristic inspection of the results indicated that only the number of species in the plot and rosette diameter in the fall were significant covariates. A test of the reduced model, containing only these covariates allowed confirmation of the equality of slopes ($F_{4,62} = 1.20$; $p = 0.32$) and indicated no difference in the adjusted group means ($F_{2,66} = 2.19$; $p = 0.12$). Means and standard errors are presented in Table 4.6. The regression was highly significant ($F_{2,66} = 39.00$; $p<0.001$). Fall rosette diameter was the most important covariate ($b = 1.50$; $t_{68} = 8.54$; $p<0.001$). Thus rosette diameter in the fall was a good predictor of rosette diameter the following summer but once adjusted for initial rosette diameter, no difference between the habitat means was evident. Number of species

Figure 4.5 Frequency distributions of rosette diameter (in centimetres) in June 1981 for seedlings that emerged in 1980. Distributions are shown by habitat and cohort. Cohort 1 emerged in the early season (approximately up to mid-June); Cohort 2 emerged in mid-season; and Cohort 3 emerged in September.


15
10
5
COHORT 3
COHORT 2
COHORT 1
DUNE RIDGE
10
5
SLACK
15
10
5
TRANSITION ZONE
NUMBER OF SEEDLINGS
1·75 3·75 5·75 7·75 9·75 11·75 13·75 15·75 17·75
ROSETTE DIAMETER CLASS MIDPOINT (cm)

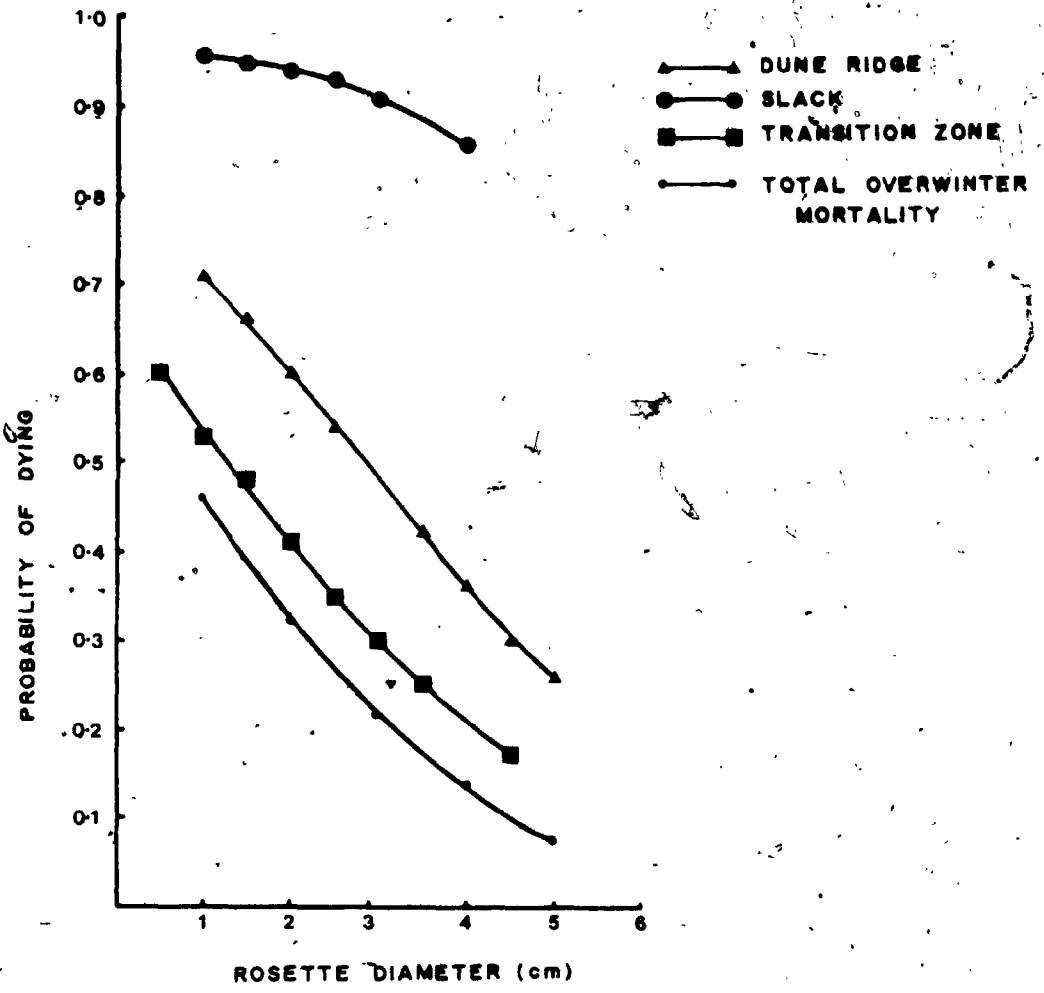
present was also significant ($b = 0.49$; $t_{68} = 2.47$; $p<0.05$). Examination of the scatter plots and residuals of June rosette diameter and number of species within each habitat indicated a strong relationship for this covariate only in the transition zone. Number of species covaried directly with rosette diameter within this habitat.

4.3.3.3. The effect of rosette diameter on the probability of dying

The relationship between rosette diameter, habitat and probability of dying is shown in Figure 4.6. Rosette diameter was the only significant predictor of overwinter mortality in the regression of probability of dying on rosette diameter, cohort and habitat. The data fit the model well ($p = 0.61$). The linear function q of the final regression equation was $q = 0.39 - 0.56R$ where R is rosette diameter. A larger rosette diameter significantly decreased the probability of dying.

The regression equation for the probability of dying within the first year on the same predictor variables provided $q = 1.91 - 0.49R - 1.30H1 + 1.84H2$ where H1 and H2 are habitat variables relating to the transition zone and slack respectively. (The coefficient for the dune ridge, "H3", is the negative sum of H1 and H2.) The cohort variable was not significant. The other coefficients were significant at $p<0.05$. The overall fit to the model was $p = 0.25$. Large rosette diameter again decreased the probability of dying. Mortality was highest in the slack, which agrees well with other analyses. Mortality was lowest in the transition zone but the difference between mortality in the transition zone and dune ridge was not great.

Figure 4.6 Regression curves showing the relationship between the probability of dying and rosette diameter, from the logistic regression of the probability of dying on habitat, cohort and rosette diameter. The top three curves show mortality over the full first year within each habitat. The lower curve shows mortality only over the winter season.


DUNE RIDGE
SLACK
TRANSITION ZONE
TOTAL OVERWINTER MORTALITY
PROBABILITY OF DYING
1·0
0·9
0·8
0·7
0·6
0·5
0·4
0·3
0·2
0·1
1
2
3
4
5
6
ROSETTE DIAMETER (cm)

4.4 Discussion

The strong connection between the mean number of emerged seedlings per plot and the detection of aggregation indicates that when many seedlings emerged, they did so in clumps. Aggregated spatial distribution of this nature is a reflection of nonrandom dispersal and/or nonrandom distribution of "safe sites" (Harper, Williams and Sagar 1965). In a sessile organism with no apparent dispersal mechanism ("censer" dispersal, Salisbury 1975) we expect most seeds to be distributed near the parent plant, and thus to show spatial nonrandomness. Eighty-five percent of the seeds of *Artemisia herba-alba* were found to fall directly beneath the parent plant canopy (Friedman and Orshan 1975). If safe sites are nonrandomly distributed, we again expect aggregated spatial distributions. The data are not available in this study to distinguish between the two. In either case, nonrandomness in spatial distribution indicates seedling-scale patchiness in the environment. There were no obvious differences in spatial patch size between habitats using seedling emergence as a measure.

When few seedlings emerged, their emergence appeared to be spatially random. However the detection of pattern is in part a function of quadrat size (Elliot 1977; Pielou 1977) and it must be concluded that, if pattern exists at low levels of emergence, the patch size is smaller than a square metre.

The detection of temporal aggregation indicates that the emergence flushes apparent from Figures 4.1a and 4.1b are statistically real. Many plants in seasonal environments have physiological mechanisms which inhibit germination during predictably unfavourable periods (Angevine and Chabot

1979). In xerophytes, germination is often cued by heavy rainfall and some other seasonality cue, such as moderate to low temperature or daylength, thus allowing avoidance of midsummer drought periods. There may be an interaction of this nature in populations of *A. campestris* at the Pinery. Periods of heavy rain in the spring and fall were followed by emergence flushes. Midsummer rains, though fairly well distributed in 1980 and 1981, prompted only limited emergence. Within this general pattern in 1980 the spring was wetter than the fall, and there was a heavier emergence flush in the spring of that year than in the fall. The fall of 1981 was unusually wet. The emergence flushes in the fall relative to the spring reflect this. The timing of rainfall during this overall pattern may also be critical. Heavy rains occurred in 1980 towards the end of September, and in 1981 at the beginning of the month, and fall emergence was much greater overall in 1981 than 1980.

It is obvious from examining overall seasonal emergence that the interaction between rainfall and temperature is only a partial determinant of regeneration during a given year. In the transition zone, the number of seedlings which emerged was approximately the same for both years. In the dune ridge, the number emerged in 1980 was over twice the number in 1981, though this was not statistically significant. This indicates that 1980 was at least as favourable a year for emergence as 1981, with respect to environmental factors. Emergence in the slack was twenty-five times as great in 1981 as 1980, though one site showed a decrease and one site no statistical change. An explanation for this may be sought in the variability of seed source availability. If historical events have decimated the potential

parent population of the 1980 cohorts in the slack, such as the severe drought of 1978, the seed population available during 1980 may have been severely limited (section 6.3.3).

In old field systems, the presence of vegetation has been shown to inhibit emergence (Fenner 1978; Holt 1972; Johnson and Thomas 1978; Tremlett et al. 1984), especially in small-seeded species (Gross 1984). The presence of litter, and in particular, quackgrass litter, depressed emergence in *Dipsacus sylvestris* (Werner 1977). In a young sand dune system, the number of other species present in a plot not only measures diversity, but also substrate stability. Its positive effect on emergence in the slack is thus not surprising, as with the combination of little ground cover and the wind corridor-effect, it is in general a highly unstable habitat. The presence of other vegetation, by providing a boundary layer of resistance to the wind, and thus a decrease in sand movement, would greatly increase the probability of an emergent's surviving long enough to be counted. The positive effect of density of other conspecifics in the transition zone may be either an indication of species-specific patch suitability or the result of the presence of reproductive plants in that plot in the recent past. Neither of these two variables affected emergence on the dune ridge, implying other factors swamped their influence, or a relative homogeneity of these factors within this habitat.

The period immediately following emergence is generally thought to be the most vulnerable stage in a (germinated) plant's life (Harper 1977). Deevey Type III survivorship curves (Deevey 1947) were followed in all habitats by all cohorts, though mortality losses were significantly more severe in the slack than in the other habitats. Factors differentially

affecting survivorship among habitats were associated with the summer season, since there was no difference among habitats in mortality over the winter period. Higher air and soil temperatures and sparse vegetation in the slack (Table 3.1) suggest desiccation as a significant mortality factor. Drought has been singled out as one of the most important factors in seedling mortality (Pemadasa and Lovell 1974, Maruta 1976; Johnson and Thomas 1978, Maun 1981). Vegetation cover, because of higher moisture retention in the soil beneath, may reduce the probability of desiccation during drought periods in the transition zone. A positive relationship between vegetation cover and survivorship has been found for *Hieracium* species in old fields (Johnson and Thomas 1978) and *Conium maculatum* (Tremlett et al. 1984). Canopy cover from shrubs and greater exposure to moisture-laden winds off the lake may have a similarly moderating effect in the dune ridge.

There were no differences in survivorship between seedlings emerging at different dates within the season. Results reported in the literature are somewhat equivocal. In annual species, differences among cohorts in survivorship have been found, with one cohort, often the earlier one, suffering greater mortality losses (Arthur et al. 1973; Marks and Prince 1981). In two species of perennial *Rumex* Weaver and Cavers (1979) found that the apparent differences in mortality could be related to a difference in time of exposure to mortality risks, and not to actual differences in mortality rates. In plants with a significant juvenile phase, it is important to compare equivalent time periods, i.e. to look at rates, over the first month or year, to equalize the effect of time of exposure. When this is done, survivorship

differences between cohorts often disappear (Weaver and Cavers 1979) or become confounded with size effects.

Several studies have shown that larger size is positively related to individual survival (Werner 1975; Gross 1981; Gross and Werner 1983). Size is often a function of date of emergence both between discrete cohorts and within a cohort (Ross and Harper 1972, Cook 1980; Fowler 1984). In *A. campestris* populations, size positively affected survivorship. Cohorts differed in mean rosette diameter at the end of their first growing season. By the beginning of the second season, cohort was no longer important in size determination, partly because small plants (primarily from Cohort 3) did not survive the overwinter period as well as large ones. The critical early establishment period for this cohort was subsumed in the overwinter period. The rosette diameter in the early summer was (not unexpectedly) closely related to that of the previous fall, overshadowing the cohort effect. A small plant from Cohort 1 would thus be "equal to" a large plant from Cohort 3. Overlapping size distributions support this. The important predictive element was size and not date of emergence directly.

Density depressed the size of individual seedlings, suggesting limited resource availability. Number of other species present was not associated with size. Competition for resources at the seedling level appears to be limited to conspecifics.

If (1) larger size is a predictor of shorter generation time (see Chapter 5), and (2) early emergents are generally larger than late ones, and (3) survivorship does not differ, then the question of why all seedlings don't

emerge in the spring becomes nontrivial. In studies of emergence date differences in annuals, higher mortality in early emergents is often associated with higher fecundity in those that survive. The later cohort is seen as "insurance" against total loss of the early cohort (Marks and Prince 1981). Early and late germinating seeds are produced on the same parent plant in populations of *Papaver dubium*, and germination differences are genetically determined (Arthur et al. 1973). In the case of *A. campestris* at Pinery Provincial Park the explanation may lie in the evolutionary history of the species, as there is much evidence that, within certain moderate temperature ranges, germination responses of widely separated populations of some species may be very similar (Thompson 1973). These germination responses may reflect conditions not visible at the present time under prevailing conditions at the study area. The other possible explanation may be that 1980 and 1981, both moderate summers, do not reflect the presence of larger scale temporal uncertainty in the environment. Years in which one cohort acts as an insurance against failure either in emergence or survival of another cohort may exist. Emergence patterns in the slack, with the very large variance between years, support this hypothesis.

## 4.5. Summary

1. Seedling emergence ranged from $0.33m^{-2}$ to $42.83m^{-2}$ within plots over a season. Detection of spatial pattern depended in part on a high number of seedlings emerging, though this relationship was not consistent. Emergence flushes occurred in the spring and fall, with little mid-season emergence, and was related to

rainfall.

2. Overall seasonal emergence within habitats ranged from $0.8m^{-2}$ to $17.8m^{-2}$ with means of 3.2 and $1.8m^{-2}$, 0.8 and $17.8m^{-2}$, and 2.5 and $2.4m^{-2}$ in the dune ridge, slack and transition zone in 1980 and 1981 respectively. There were no differences among sites and between years in the dune ridge and transition zone. Emergence was affected by number of other species present in the slack and by density of juvenile conspecifics in the transition zone.

3. Seedling mortality followed a Deevey Type III curve in all habitats. Survivorship to the beginning of the second season was 0.49 in the dune ridge, 0.27 in the slack and 0.48 in the transition zone.

4. By the end of the first growing season, seedlings in the dune ridge were larger than those in the slack and transition zone, adjusted for cohort. Seedlings from earlier cohorts were larger than those from later cohorts, and plants in high density plots at emergence were smaller. Fall rosette diameter, independent of cohort, affected rosette diameter at the beginning of the second growing season. Adjusted for the difference in initial size, there were no differences in mean rosette diameter among habitats. Number of species in the plot positively affected rosette diameter in the transition zone.

5. Larger rosette diameter was associated with increased survivorship both overwinter and over

a full year. Cohort, independent of size, did not affect survivorship. Adjusted for rosette diameter, there were no differences among habitats in overwinter mortality, but mortality over the first year was highest in the slack.

# CHAPTER 5

# GROWTH AND SURVIVAL IN THE JUVENILE PHASE

## 5.1 Introduction

With the exception of the periods directly after emergence flushes, the juvenile (rosette) phase comprises the largest proportion of visible plants in a perennial monocarpic population such as *Artemisia campestris*. The subject of this chapter is the juvenile phase, defined as the period starting with the plant's second growing season and ending at flowering. It is the time of active and visible growth, the magnitude and rapidity of which will affect the plant's future reproductive success.

Size distributions of plants in a population tend to be lognormal (Harper 1977), with a large number of relatively small plants and a few larger individuals, though bimodal distributions have been reported in seedlings (Rabinowitz 1979). Size distributions are potentially affected by differential growth rates (Rabinowitz 1979; Mithen, Harper and Weiner 1984) and size-dependent mortality (Obeid, Machin and Harper 1967; White and Harper 1970; Mithen, Harper and Weiner 1984). Growth rates in turn are influenced by resource availability (White and Harper 1970; Solbrig, Newell and Kincaid 1980; Solbrig 1981), genotype (Solbrig, Newell and Kincaid 1980; Jefferies,

Davy and Rudmick 1981), herbivory (van der Meijden and van der Waals-Kooi 1979) and emergence order (Ross and Harper 1972). Growth rates may vary within a season (Boorman 1982) and this pattern may reflect habitat differences (Jefferies, Davy and Rudmick 1981).

Within the *A. campestris* complex the presence of multiple stems has been used as a diagnostic character in determining subspecies (Chapter 2). Both single-stemmed and multiple-stemmed plants occur at Pinery Provincial Park but investigation of other features indicated that only one taxon was present. Therefore it seemed of general interest to determine what, if any, environmental factors affected the development of multiple stems in *A. campestris* at the study site. This was included in the study of growth patterns.

There are two alternative routes "out" of the juvenile phase, mortality and flowering. The relative importance of age and size in predicting which of these fates will occur has aroused increasing interest in plant population biologists in recent years (Werner 1975; Werner and Caswell 1977; Baskin and Baskin 1979a,b; Gross 1981, Law 1981; Hirose and Kachi 1982). Mortality in juvenile plants tends to be lower than that in seedlings and fairly constant with age (Sarukhan and Harper 1973; Hett 1971; Harper 1977, Silvertown 1982), though it is often size dependent (Solbrig, Newell and Kincaid 1980; Fowler and Antonovics 1981; Newell, Solbrig and Kincaid 1981; Solbrig 1981). The relationship between age and flowering has been shown to be tenuous in several monocarpic perennials due to differences in growth environment (Gross 1981), nutrient status (Hirose and Kachi 1982), shading (Werner 1975) and diversity of associated flora (Werner 1977). Habitat type

affects the length of time required to reach critical size for flowering. Holt (1972) and Gross (1980) showed that biennials growing in one year old fields had higher probabilities of flowering in their second year than those in older fields.

Delayed reproduction greatly affects the reproductive success of individuals (Bell 1976, 1980). Given monocarpy and an equal probability of survival to reproduction, a plant which flowers in its third year will have to produce (S exp 3/2) the number of seeds S produced by a plant flowering in its second year to be equal in fitness (Hart 1977; Gross 1980; Silvertown 1983).

In a facultative polycarp such as *Artemisia campestris* a difficulty arises in how to classify plants that are in a post-flowering vegetative phase. In this study I have treated them as a separate phase unless otherwise indicated.

This chapter will address the following questions:

1. What is the size distribution of the juvenile phase?
2. Do growth rates differ between habitats within a season, and what are the effects of age, density and herbivore damage?
3. Does growth rate over a year differ between habitats?
4. What proportion of the population develops multiple stems? Is this affected by damage to the

plant, habitat or age?

5. What is the probability of survival during the juvenile phase, and how is survival affected by size, age, herbivore damage and habitat?

6. What is the probability of transition from the juvenile phase into the reproductive phase, and how is it affected by age, size and habitat?

7. What is the duration of the juvenile phase and does the duration differ between habitats?

## 5.2 Materials and Methods

### 5.2.1. General methods

See Chapter 3 for details on sampling techniques. Rosette diameters were measured to the nearest half centimetre with a meter stick at monthly intervals from July to October in 1978, and at six-week intervals from the beginning of May to the end of September in 1979 and 1980. These dates correspond to the initiation of recognizable phenological phases beginning of seasonal growth, bolting, anthesis and end of seasonal growth. In 1981, data were recorded in mid-June and late September only. Rosette diameters of all plants within this study were recorded.

Ages were assigned to plants in the following way. Plants marked at recruitment in 1979 and 1980 were assigned Age 0 to indicate their first growing season. Thus these plants reached Age 1 (one year old) in 1980 and 1981 respectively, and the 1979 sample reached Age 2 in 1981. Rosette size distributions from these known age samples were then compared with size

distributions of the plants tagged in 1978 and an approximate Age I assigned to these plants based on 95% confidence intervals (Appendix II). No attempt was made to age plants extant in 1m x 1m plots established in 1980.

Density within each 1m x 1m plot was calculated from data collected at the beginning of the growing season (May) and included only juvenile plants. Counts including seedlings were thought to be too labile and not biologically relevant as a measure of intraspecific competition within juvenile populations.

Herbivore damage included browsing and trampling by vertebrates and infestation by insects resulting in destruction of plant tissue, particularly the meristem. Presence of insects was also noted, but only plants with visibly affected tissue were considered damaged.

The reciprocal transplant-replant and common garden experiment is described in Chapter 3.

5.2.2. Distribution of rosette diameters

The shape and location of the rosette diameter distribution within each habitat was investigated using BMDP2D. Location estimates and measures of skewness and kurtosis were found for data from 1m x 1m plots at each recording date in 1980. Histograms of these distributions were produced using MINITAB.

5.2.3. Growth

5.2.3.1. Growth within a season

Patterns of growth within a season among habitats were explored via an analysis of covariance (BMDP1V). Rosette diameter in each of June, August and September 1980 were analysed using the rosette diameter from the previous recording period (May, June and August respectively) within each habitat as a covariate. Time period (beginning of the season, mid-season or end of season) was used as a grouping variable. This sample included only those plants which survived the entire season to avoid confounding differences in growth patterns with possible differences in mortality patterns. The data did not require transformation.

5.2.3.2. Growth within a year

Yearly increase in rosette diameter was used as a measure of relative growth. An analysis of covariance of September rosette diameter among habitats, with rosette diameter from the previous fall, age (1-5), number of stems, and damage (1,0) as covariates, was performed using BMDP1V. Age 1 plants were included because the period analysed covered their second growing season, not discussed in Chapter 4. Rosette diameter was $\log_e$ transformed. Damage was deleted as a covariate after preliminary analysis revealed its presence only in older age groups. This produced singular matrices and thus disallowed a test of the equality of slopes among groups. The analysis of covariance was followed by a Student-Newman-Keuls comparison of means test for unequal sample sizes on the adjusted means

(Sokal and Rohlf 1969).

5.2.3.3. Development of multiple stems

The development of multiple stems was hypothesized to be related to any one of the following factors damage to the plant, habitat, age and rosette diameter. Stem frequency was coded as 1 (single stemmed) or 2 (multiple stemmed) because of small sample sizes in larger stem-number classes. A logistic regression (BMDPLR, see also section 4.2.4) with damage, age, rosette diameter, habitat and their interactions as regressor variables was performed.

5.2.4. Survival

The probability of surviving (1 = dead, 0 = survived or flowered ) within a year was regressed (BMDPLR) on habitat, age (1-4, predicting survival to age 2-5), rosette diameter at the beginning of the period covered, and the interactions among these variables. Preliminary analysis showed no relationship between damage, number of stems and survival.

Year was not included as a variable as it was highly confounded with age due to the sampling technique. In 1978 only Age 2 plants were sampled, but Age 2 plants were also present in the 1980 sample though in small numbers. The 1979 sample contained only Age 1 and Age 3 plants. Preliminary analysis within 1980 (not shown), a year containing Ages 1, 2 and 4, indicated differences among ages within a year, and thus it was decided to pool across years using the age variable, with some caution in interpretation.

Expected probabilities of survival, based on mean rosette diameter within each age class, were calculated and compared to observed proportions surviving.

### 5.2.5. Probability of flowering

The probability of flowering was also analysed using logistic regression (BMDPLR) with flowering (coded 1) as an alternative state to dying and remaining vegetative (coded 0). Habitat, age (1-4), rosette diameter and their interactions were used as regressor variables. Rosette diameter from the previous September was used to predict flowering the following season, as preliminary analysis showed a closer relationship between the two than with rosette diameters at other periods. Year was not used as a variable for the reasons given in the previous section.

From the raw data a minimum size and age observed for flowering was assessed for each habitat. The regression model allowed calculation of a quantity called here the RD50, the rosette diameter at which 50% of the juvenile plants within a habitat can be expected to flower. Calculation involved substitution into the final model of an expected probability of 0.5 for flowering and solving for the unknown rosette diameter. Expected probabilities of flowering for each age class were calculated using mean rosette diameter within the age class. Expected probabilities were then compared to the actual proportions which flowered.

5.2.6. Duration of the juvenile phase

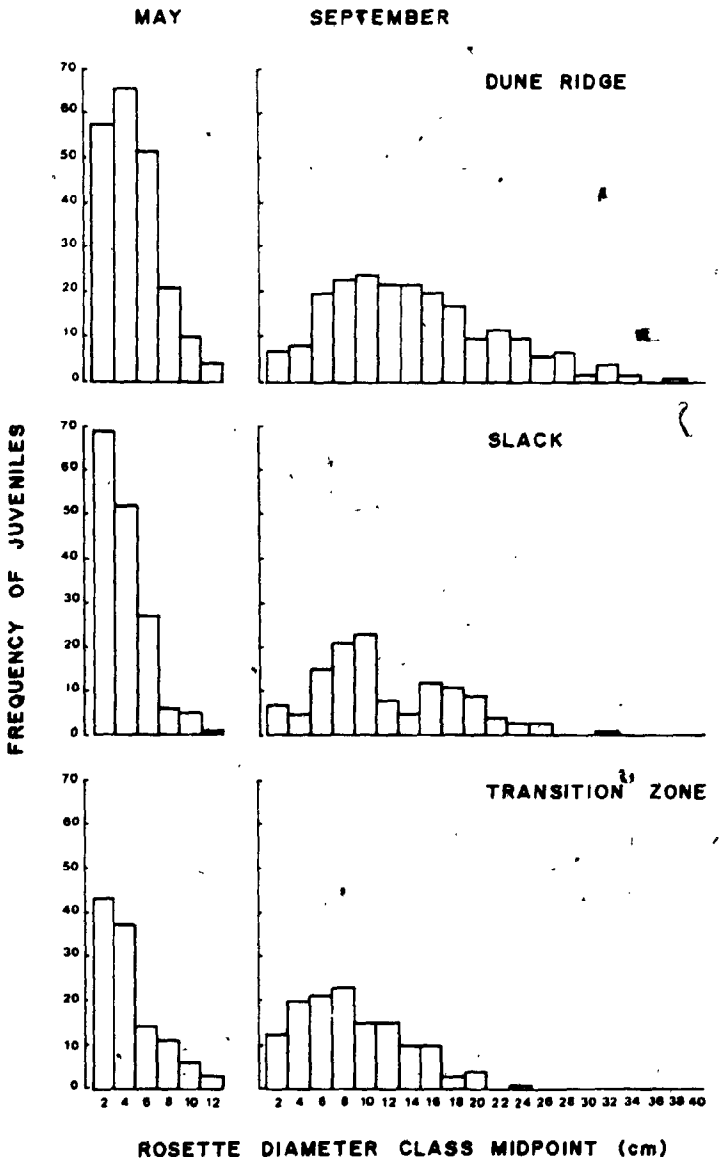
The probability of transition $p(t_x)$ into the age class x as a juvenile plant was calculated as $p(s_x) \times (1-p(f_{x-1}))$ where $p(s_x)$ is the probability of survival to age x and $p(f_{x-1})$ is the probability of flowering at age x-1. The cumulative probability of remaining juvenile in each age class can then be calculated as $\Pi\, p_x(t)$ where x is the oldest age class. Survival to Age 2 was adjusted to include survival during the first year of life (Chapter 4). The conditional probability of remaining vegetative in each age class gives the proportion of surviving plants within each age class expected to remain juvenile and thus provides a comparative measure of the duration of the juvenile phase.

5.3 Results

5.3.1. Rosette size distribution

Rosette size distributions of all non-seedling plants present in the 1m x 1m plots in May and September 1980 in each of the three habitats are shown in Figure 5.1. Descriptive statistics of the May, June, August and September distributions are presented in Tables 5.1 and 5.2. Distributions were similar in all habitats in May, with means of approximately 4 cm and variances slightly higher. Although all distributions were strongly skewed in May none showed evidence of bimodality. The slack distribution was significantly leptokurtic in May, and this was the only instance of significant kurtosis in any habitat in any month. By September the mean rosette diameter had increased to 14.19cm ± 1.00 (standard error) in the

Figure 5.1 Rosette diameter size class distribution (in cm) of all juvenile plants in 1m x 1m plots during May and September 1980 in the dune ridge, slack and transition zone habitats.


MAY
SEPTEMBER
DUNE RIDGE
SLACK
TRANSITION ZONE
FREQUENCY OF JUVENILES
0
10
20
30
40
50
60
70
2 4 6 8 10 12
2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32 34 36 38 40
ROSETTE DIAMETER CLASS MIDPOINT (cm)

## CENTRAL TENDENCY

| | MONTH | n | MEAN (cm) | $s^2$ | MEDIAN (cm) | MODE (cm) |
|---|---|---|---|---|---|---|
| DUNE RIDGE | MAY | 211 | 4.50 | 5.59 | 4.00 | 2.00 |
| | JUNE | 231 | 8.27 | 20.26 | 8.00 | 7.00 |
| | AUG. | 226 | 12.78 | 46.03 | 11.50 | 5.00 |
| | SEPT. | 217 | 14.19 | 55.48 | 13.00 | 12.00 |
| SLACK | MAY | 163 | 3.50 | 4.62 | 3.00 | 2.50 |
| | JUNE | 145 | 7.24 | 15.23 | 6.50 | 4.00 |
| | AUG. | 132 | 11.56 | 38.95 | 10.00 | 10.00 |
| | SEPT. | 127 | 11.80 | 37.67 | 10.00 | 10.00 |
| TRANS-ITION ZONE | MAY | 114 | 4.04 | 6.70 | 3.50 | 2.00 |
| | JUNE | 146 | 6.84 | 18.96 | 6.00 | 4.00 |
| | AUG. | 137 | 8.16 | 24.05 | 7.50 | 6.00 |
| | SEPT. | 134 | 8.60 | 23.49 | 8.00 | 5.00 |

Table 5.1 Measures of central tendency and variance of rosette diameter distributions of juvenile plants in 1m x 1m plots in the dune ridge, slack, and transition zone at four recording periods in 1980.

SHAPE

| | MONTH | n | SKEW-NESS | SIGN. | KURT-OSIS | SIGN. |
|---|---|---|---|---|---|---|
| DUNE RIDGE | MAY | 211 | 0.79 | *** | 0.15 | NS |
| | JUNE | 231 | 0.76 | *** | 0.07 | NS |
| | AUG. | 226 | 0.60 | *** | -0.25 | NS |
| | SEPT. | 217 | 0.61 | *** | -0.18 | NS |
| SLACK | MAY | 163 | 1.29 | *** | 2.10 | *** |
| | JUNE | 145 | 0.66 | ** | -0.21 | NS |
| | AUG. | 132 | 0.65 | ** | 0.35 | NS |
| | SEPT. | 127 | 0.58 | ** | -0.31 | NS |
| TRANS-ITION ZONE | MAY | 114 | 1.02 | *** | 0.09 | NS |
| | JUNE | 146 | 0.70 | *** | -0.55 | NS |
| | AUG. | 137 | 0.86 | *** | 0.70 | NS |
| | SEPT. | 134 | 0.61 | ** | -0.35 | NS |

Table 5.2 Skewness and kurtosis of the rosette diameter distribution of juvenile plants in 1m x 1m plots located in the dune ridge, slack and transition zone at four recording periods in 1980. Significant deviations from normality are indicated by * ($p \leq 0.05$); ** ($p \leq 0.01$); *** ($p \leq 0.001$); NS not significant.

dune ridge, 11.80 ± 1.07 in the slack and 8.60 ± 0.83 in the transition zone. Larger means were accompanied by greater ranges and higher variances within habitats. The slack population also showed bimodality in September. Skewness decreased in all habitats as the season progressed (Table 5.2).

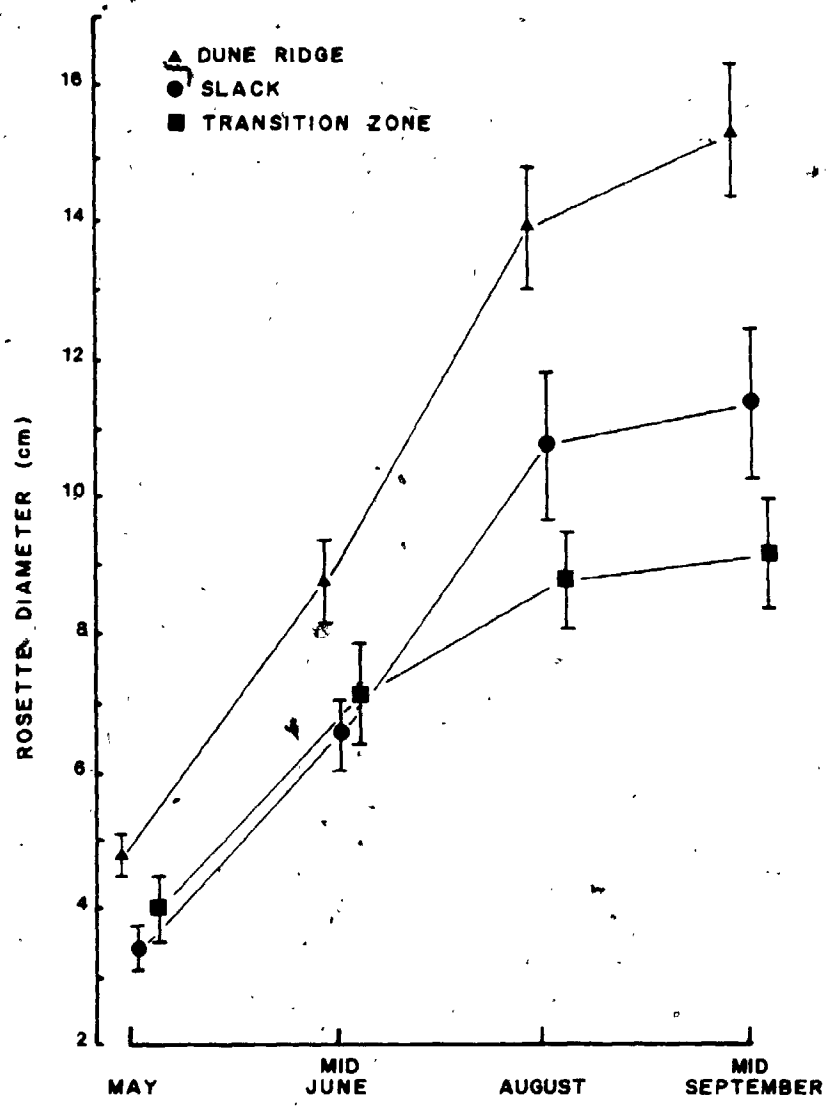
5.3.2. Growth

5.3.2.1. Growth within a season

Means and standard errors of rosette diameters in May, June, August and September 1980 are shown in Figure 5.2. These means differ from the ones in the previous section since they include only those plants which survived the entire season. The same trends are apparent. The relative differences in rosette diameter between habitats increased over the season. The increase at the beginning of the season appeared to be proportional among habitats. The increase in the mid-season period appeared similar in the slack and the dune ridge, but showed a relatively smaller increase in the transition zone. The rosette diameter of plants in all habitats stabilized in August and showed only a relatively small increase later in the growing season.

The results of the analysis of covariance of rosette diameter among time periods are shown in Table 5.3. Within the dune ridge, the slopes among time periods were not equal ($F_{2,604} = 24.72$; $p < 0.001$). The relationship between rosette diameter in May and rosette diameter in June was stronger than that in the June-August period, which in turn was stronger than that of the final period. Rosette diameter increase in the dune ridge occurred most

Figure 5.2 Means and standard errors of rosette diameter in centimetres at the beginning of May, mid-June, beginning of August and mid-September 1980. Sample includes only those juvenile plants which survived from May to September.


DUNE RIDGE
SLACK
TRANSITION ZONE
ROSETTE DIAMETER (cm)
16
14
12
10
8
6
4
2
MAY
MID JUNE
AUGUST
MID SEPTEMBER

| | | | SLOPE | ROSETTE DIAMETER |
|---|---|---|---|---|
| | PERIOD | n | b | $\bar{X}$(cm) ± S.E. |
| DUNE RIDGE | MAY-JUNE | 191 | 1.59 | 8.82 ± 0.30 |
| | JUNE-AUG. | 212 | 1.25 | 12.98 ± 0.26 |
| | AUG.-SEPT. | 207 | 0.92 | 14.23 ± 0.29 |
| SLACK | MAY-JUNE | 106 | 1.41 | 7.09 ± 0.29 |
| | JUNE-AUG. | 110 | 1.42 | 11.29 ± 0.26 |
| | AUG.-SEPT. | 118 | 0.96 | 12.01 ± 0.28 |
| TRANSITION ZONE | MAY-JUNE | 107 | 1.45 | 7.24 ± 0.25 |
| | JUNE-AUG. | 129 | 0.99 | 8.33 ± 0.22 |
| | AUG.-SEPT. | 132 | 0.90 | 8.63 ± 0.22 |

Table 5.3 Slopes within a season (b), rosette diameter means ($\bar{X}$) and standard errors (S.E.) derived from the analysis of covariance between habitats of rosette diameter at time $t_{x+1}$ using rosette diameter at time $t_x$ as a covariate.

rapidly at the beginning of the season, with a gradual slowing down of the process throughout the summer.

In the slack, the slopes among time periods were again unequal ($F_{2,328}$ = 23.36; $p<0.001$). The slopes in the beginning and mid-season periods were nearly equal and higher than the slope in the August-September period. The period of rapid growth lasted longer in the slack than in the dune ridge.

In the transition zone the slopes were also unequal ($F_{2,362}$ = 14.62, $p<0.001$), but here the relationship between rosette diameters in contiguous periods was strongest at the beginning of the season, with slopes at the middle and end of the season nearly equal. Rapid growth occurred only at the beginning of the season in the transition zone.

5.3.2.2.Growth over a year

Raw means, standard errors and means of $\log_e$ transformed rosette diameter for the sample used in the analysis of covariance of yearly increase in rosette diameter are presented in Table 5.4. This table also contains the adjusted group means calculated from the analysis. The hypothesis of the equality of slopes among groups was accepted ($F_{6,386}$ = 1.72; p = 0.11) but that of zero slope was rejected ($F_{3,392}$ = 290.15; $p<0.001$). All covariates were highly significant (Table 5.5) with previous year's rosette diameter having the most influence. Thus, initially larger plants, older plants and plants with more than one stem had larger final rosette diameters. There were no significant interactions. The hypothesis of the equality of group means

ROSETTE DIAMETER (cm)

| HABITAT | n | $\bar{X} \pm$ S.E. | $LOG_e \bar{X} \pm$ S.E. | ADJ. $\bar{X}$ |
|---|---|---|---|---|
| DUNE RIDGE | 101 | 17.07 ± 0.53 | 2.17 ± 0.04 | 2.22 |
| SLACK | 53 | 17.10 ± 0.67 | 2.22 ± 0.05 | 2.02 |
| TRANSITION ZONE | 244 | 11.80 ± 0.32 | 2.06 ± 0.03 | 2.09 |

Table 5.4 Raw means ($\bar{X}$), means of $\log_e$ rosette diameter ($LOG_e \bar{X}$), adjusted means (ADJ. $\bar{X}$) and standard errors (S.E.) derived from the analysis of covariance of rosette diameter increase over year among habitats with previous year's rosette diameter, age and number of stems as covariates.

| COVARIATE | b | S.E. | t | SIGN. |
|---|---|---|---|---|
| AGE | 0.31 | 0.02 | 13.59 | *** |
| STEMS | 0.09 | 0.01 | 6.07 | *** |
| LOGERD1 | 0.58 | 0.04 | 14.69 | *** |

Table 5.5 Regression coefficients (b), standard errors (S.E.) and t statistics derived from the analysis of covariance of rosette diameter among habitats with age, number of stems, and the previous year's loge transformed rosette diameter (LOGERD1) as covariates. Significance of the coefficients: * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$.

was rejected ($F_{2,392} = 5.59$; $p = 0.004$). The comparison of means tests indicated that dune ridge plants had a significantly larger mean rosette diameter, adjusted for age, number of stems and initial rosette diameter, and thus a greater increase in rosette diameter over the period studied, than plants in the other habitats.

5.3.2.3. Development of multiple stems

The distribution by habitat of single-stemmed and damaged juvenile plants is presented in Table 5.6. Single stemmed plants occurred most frequently in the dune ridge, and plants in that habitat suffered the least damage. The distribution of both variables in the transition zone and slack was similar, with proportionately fewer single-stemmed plants and more damaged plants than in the dune ridge.

Table 5.7 contains the joint distribution of age, number of stems and damage. The percentage of plants with single stems decreased with age until Age 5. The association of damaged plants with multiple stems was clearest in the Age 3 and Age 4 groups and least clear in Age 5.

The final results of the regression of the probability of having a single stem on age, rosette diameter, damage, habitat and their interactions is presented in Table 5.8 (see Appendix III for an explanation of design variable coding). The fit of the data to the model was adequate ($\chi^2 = 3.67$; $p = 0.28$). The intercept term was significant and positive in sign. Thus the overall probability of having a single stem was significantly lower than 0.5. The presence of visible damage was the most significant factor in predicting

| HABITAT | % SINGLE-STEMMED | % DAMAGED |
|---|---|---|
| DUNE RIDGE | 76.2 | 13.9 |
| SLACK | 64.2 | 41.5 |
| TRANSITION ZONE | 61.0 | 41.0 |

Table 5.6 The percentage of single-stemmed plants and plants with visible tissue damage in each of three habitats. n = 398.

| | SINGLE-STEMMED | MULTI-STEMMED | | TOTAL |
|---|---|---|---|---|
| | % DAMAGED | % DAMAGED | % 1 STEM | % DAMAGED |
| AGE 1 | 3.8 | 50.0 | 96.3 | 5.5 |
| AGE 2 | 5.3 | 35.7 | 80.3 | 11.3 |
| AGE 3 | 35.1 | 62.3 | 55.9 | 47.1 |
| AGE 4 | 29.1 | 66.7 | 50.0 | 47.9 |
| AGE 5 | 38.5 | 12.5 | 62.0 | 28.6 |

Table 5.7 The proportion of damaged individuals among single- and multi-stemmed plants of different ages, in three habitats. n = 244.

| REGRESSOR | b ± S.E. | t | SIGNIFICANCE |
|---|---|---|---|
| AGE(1) | -0.44 ± 0.41 | -1.07 | NS |
| AGE(2) | -0.80 ± 0.31 | -2.58 | ** |
| AGE(3) | -0.60 ± 0.23 | -2.61 | ** |
| AGE(4) | 0.17 ± 0.31 | 0.55 | NS |
| ROSETTE DIAMETER | -0.04 ± 0.02 | -2.00 | * |
| DAMAGE | -0.62 ± 0.12 | -5.17 | *** |
| INTERCEPT | 1.44 ± 0.32 | 4.56 | *** |

Table 5.8 The regression coefficients (b), standard errors (S.E.) and t statistics from the logistic regression of the probability of having a single stem on age, rosette diameter and damage of *Artemisia campestris*. Significance of the regression coefficients: * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$; NS not significant. n = 398.

a multi-stemmed state. Plants of Age 3 or 4 had a higher probability of having multiple stems, as well as plants with larger rosette diameters. Habitat did not enter the stepwise regression. Examination of the initial statistics to enter and remove variables (not shown) indicated that once damage was entered, habitat lost importance. Differences among habitats in the number of multiple stemmed plants was related to differences in number of plants damaged in each habitat (Table 5.6).

5.3.3. Survival

The results from the logistic regression of the probability of survival in the juvenile state on rosette diameter, habitat, age and their interactions are presented in Table 5.9 and Figure 5.3. The data fit the model adequately ($\chi^2$ = 7.36; p = 0.39). Tests of the regression coefficients indicated significant interactions between the first age variable (Age 5) and rosette diameter. There was also a significant interaction between the first habitat variable (the transition zone) and rosette diameter. Increased rosette diameter either increased or showed no relation to the probability of survival in the dune ridge and slack at ages 2 through 4, and the transition zone at Age 2 (Figure 5.3). The relationship was reversed in the transition zone above Age 2 and in all habitats at Age 5, indicating larger old plants had a higher probability of dying than small plants of the same age. The strongest relationship between rosette diameter and probability of survival occurred in all habitats at Age 2. Survivorship appeared to decrease with age, though the presence of significant interactions with rosette diameter make statistical conclusions tenuous.

| REGRESSOR | b ± S.E. | t | SIGNIFICANCE |
|---|---|---|---|
| HABITAT(1) | 0.82 ± 0.31 | 2.67 | * |
| HABITAT(2) | -0.47 ± 0.34 | -1.38 | NS |
| AGE(1) | 1.38 ± 0.67 | 2.07 | * |
| AGE(2) | -0.61 ± 0.44 | -1.37 | NS |
| AGE(3) | 0.20 ± 0.40 | 0.05 | NS |
| ROSETTE DIAMETER | 0.06 ± 0.04 | 1.60 | NS |
| HR(1) | -0.50 ± 0.02 | -2.31 | * |
| HR(2) | 0.07 ± 0.02 | 0.30 | NS |
| AR(1) | -0.13 ± 0.05 | -2.48 | * |
| AR(2) | -0.06 ± 0.04 | -1.32 | NS |
| AR(3) | -0.02 ± 0.04 | -0.54 | NS |
| INTERCEPT | 0.09 ± 0.37 | 0.24 | NS |

Table 5.9 Regression coefficients (b) ± standard errors (S.E.) and t-values derived from the logistic regression of the probability of survival on habitat, age, rosette diameter and their interactions. * : $p<0.05$; NS not significant. HR(1) = HABITAT(1) x ROSETTE DIAMETER; HR(2) = HABITAT(2) x ROSETTE DIAMETER; AR(1) = AGE(1) x ROSETTE DIAMETER, etc. n = 684.

Figure 5.3 The expected probability of survival within each age class in each habitat, derived from the logistic regression of probability of survival on rosette diameter, habitat and age.

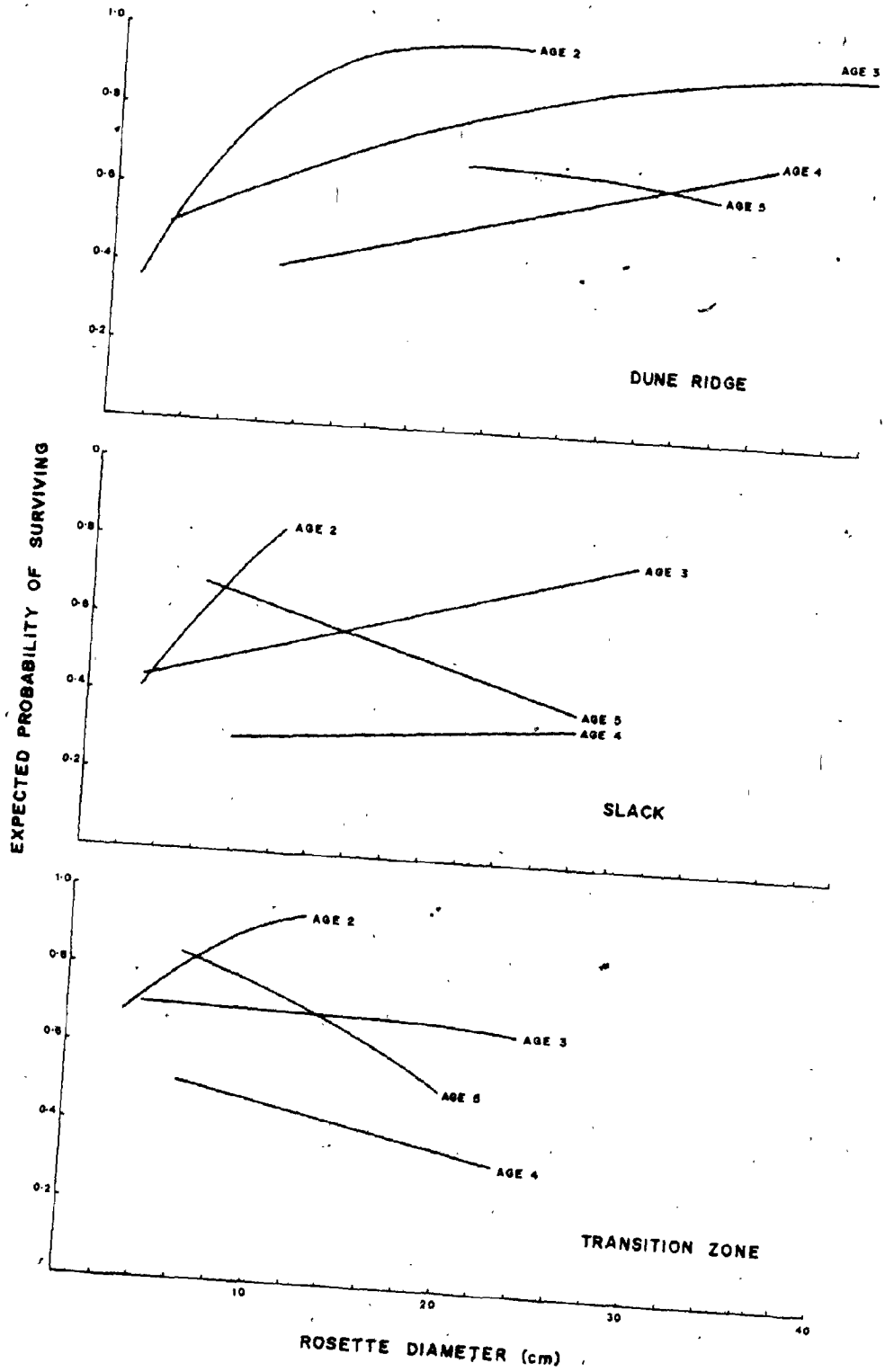

EXPECTED PROBABILITY OF SURVIVING
1·0
0·8
0·6
0·4
0·2
0
AGE 2
AGE 3
AGE 4
AGE 5
DUNE RIDGE
SLACK
TRANSITION ZONE
10
20
30
40
ROSETTE DIAMETER (cm)

Table 5.10 contains expected probabilities of survival based on the model, and observed proportions surviving calculated from the raw data. Expected probabilities were based on mean rosette diameter for each age-class in each habitat, also presented in Table 5.10. In general, expected and observed proportions surviving were within 10% of each other. Deviations larger than this occurred in the slack in all age classes except Age 3 and in the transition zone at Age 2. All these groups had small sample sizes. Deviations from normality within these small samples may have made the use of mean rosette diameter in the calculation of expected survival inappropriate. The expected probability of survival was highest at each age in the dune ridge, and lowest in the slack except at Age 5, when it was highest in the transition zone. The observed proportion surviving followed the same pattern, with the exception of Age 2, when all plants in the transition zone survived. The actual proportion surviving at Age 5 was the same in all habitats.

### 5.3.4. Probability of flowering

The results from the regression of probability of flowering on habitat, age, rosette diameter and their interactions are presented in Table 5.11 and Figure 5.4. The model fit the data adequately ($\chi^2 = 10.03$; $p = 0.26$). Rosette diameter was highly significant in predicting flowering (Table 5.11). Figure 5.4 shows a strong relationship between increased size and increased probability of flowering in all habitats. The first habitat variable was significant and positive, showing that at a given rosette diameter the probability of flowering was greater in the transition zone than in the

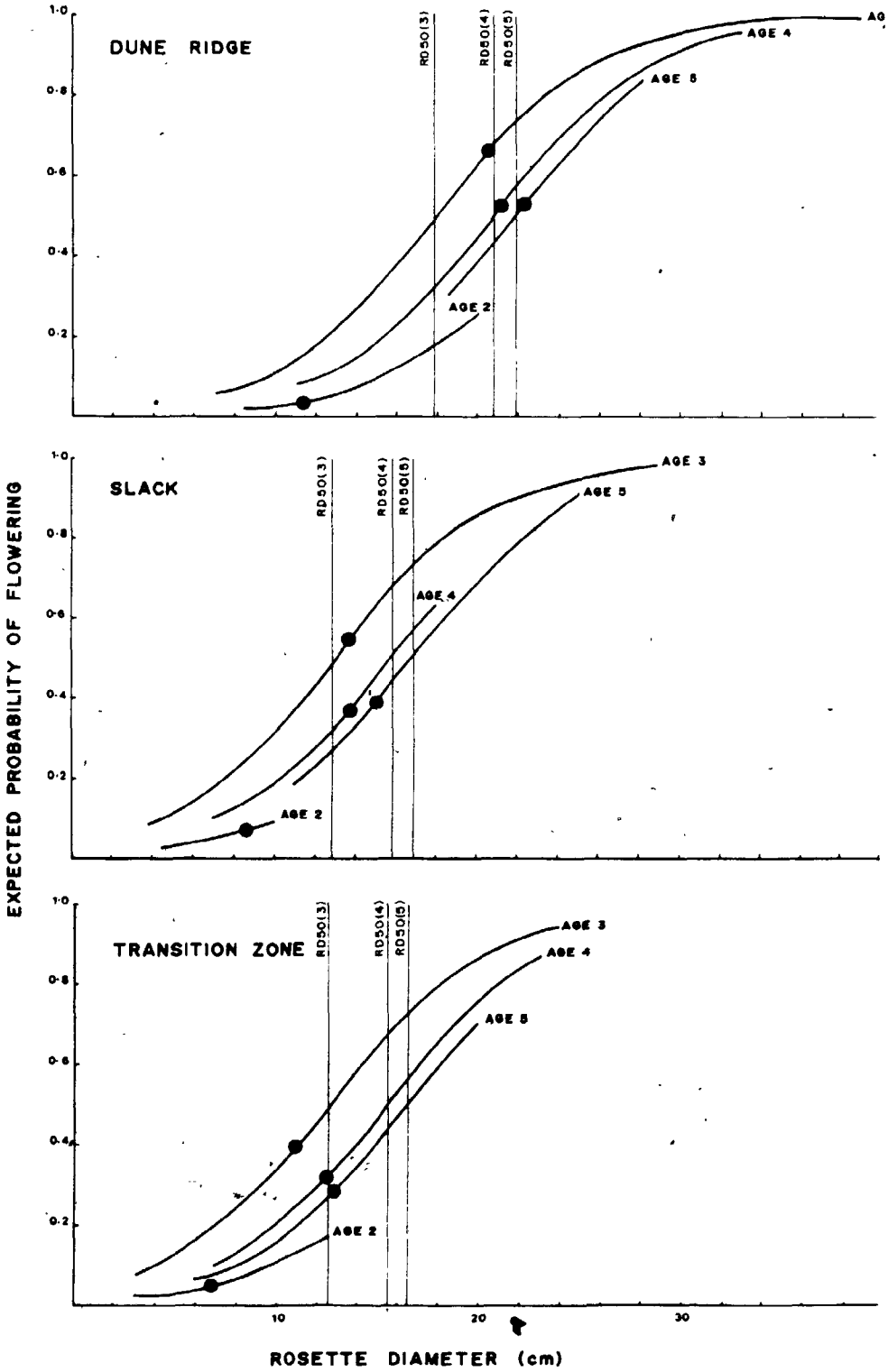
| HABITAT | TO AGE | n | $\bar{X}$ (cm) | PROBABILITY OF SURVIVAL EXPECTED | OBSERVED |
|---|---|---|---|---|---|
| DUNE RIDGE | 2 | 14 | 9.5 | 0.87 | 0.79 |
| | 3 | 114 | 19.3 | 0.80 | 0.76 |
| | 4 | 29 | 21.4 | 0.54 | 0.63 |
| | 5 | 9 | 25.6 | 0.65 | 0.67 |
| SLACK | 2 | 10 | 7.6 | 0.72 | 0.40 |
| | 3 | 102 | 12.9 | 0.56 | 0.54 |
| | 4 | 27 | 16.8 | 0.32 | 0.48 |
| | 5 | 6 | 16.8 | 0.52 | 0.67 |
| TRANSITION ZONE | 2 | 14 | 6.8 | 0.83 | 1.00 |
| | 3 | 215 | 11.0 | 0.70 | 0.72 |
| | 4 | 114 | 12.3 | 0.44 | 0.39 |
| | 5 | 30 | 12.6 | 0.71 | 0.67 |

Table 5.10 The expected probability of survival based on mean rosette diameter $\bar{X}$ within each age group based on the model derived from the logistic regression. Observed proportions surviving and sample size n are also presented.

| REGRESSOR | b ± S.E. | t | SIGNIFICANCE |
|---|---|---|---|
| HABITAT(1) | 0.48 ± 0.18 | 2.58 | ** |
| HABITAT(2) | 0.40 ± 0.21 | 1.89 | NS |
| AGE(1) | -0.17 ± 0.38 | -0.44 | NS |
| AGE(2) | 0.08 ± 0.31 | 0.25 | NS |
| AGE(3) | 0.81 ± 0.25 | 3.23 | ** |
| ROSETTE DIAMETER | 0.25 ± 0.03 | 8.36 | *** |
| INTERCEPT | -4.51 ± 0.51 | -8.81 | *** |

Table 5.11 Regression coefficients (b), standard errors (S.E.), t-values and their significance levels derived from the logistic regression of the probability of flowering on rosette diameter, habitat, age and their interactions. * $p \ll 0.05$; ** $p \ll 0.01$; *** $p \ll 0.001$. n = 429.

Figure 5.4 Expected probability of flowering in each habitat based on the logistic regression of probability of flowering on rosette diameter, habitat and age. Large dots are mean rosette diameters within age class. Lines labelled RD50(x) give the rosette diameter above which 50% of the plants in age class (x) are expected to flower.


DUNE RIDGE
SLACK
TRANSITION ZONE
RD50(3)
RD50(4)
RD50(5)
AGE 2
AGE 3
AGE 4
AGE 5
1·0
0·8
0·6
0·4
0·2
10
20
30
EXPECTED PROBABILITY OF FLOWERING
ROSETTE DIAMETER (cm)

overall sample. Only the third age variable was significant at $p<0.05$, and the sign of the coefficient was again positive. Thus the probability of flowering at Age 3 at a given rosette diameter was higher than the overall sample. The highest probability of flowering in all habitats occurred at Age 3, followed by Age 4, Age 5 and Age 2. In fact no plants under Age 3 flowered in the slack or dune ridge. Only two plants in the transition zone flowered at Age 2. This was not significantly different from the dune ridge and slack, using Fisher's Exact test ($p = 0.30$ and $p = 0.59$ respectively).

The minimum rosette diameter at which flowering was observed in the following season was 13cm in the dune ridge ($p = 0.22$ based on the model), 7cm in the slack ($p = 0.18$) and 4cm in the transition zone ($p = 0.10$). All these plants were Age 3. RD50 for all age classes within habitats can be observed from Figure 5.4. At Age 3, RD50 in the dune ridge was 18cm. In the slack and transition zone RD50 was approximately 13cm for Age 3. RD50's appeared to increase with age. Irrespective of age, RD50 for the whole juvenile population was calculated as 21cm in the dune ridge, and 16cm in the slack and transition zone. Thus plants flowered at smaller sizes in the slack and transition zone than in the dune ridge.

Table 5.12 contains the expected probabilities of flowering within each age class-habitat combination, based on mean rosette diameter for the class. It also contains the observed proportion flowering. The largest deviations of observed and expected probabilities occurred in the smallest samples. Agreement in the largest age class, Age 3, was good in all habitats. In the dune ridge the actual proportions flowering at Ages 4 and 5 were smaller than the model predicted but the trend of decreased probability of flowering

| HABITAT | AT AGE | n | $\bar{x}$(cm) | PROBABILITY OF FLOWERING EXPECTED | OBSERVED |
|---|---|---|---|---|---|
| DUNE RIDGE | 2 | 11 | 11.3 | 0.04 | 0.00 |
| | 3 | 85 | 20.5 | 0.65 | 0.65 |
| | 4 | 30 | 21.1 | 0.51 | 0.40 |
| | 5 | 6 | 22.3 | 0.52 | 0.33 |
| SLACK | 2 | 4 | 8.5 | 0.06 | 0.00 |
| | 3 | 54 | 13.8 | 0.55 | 0.48 |
| | 4 | 13 | 13.9 | 0.37 | 0.54 |
| | 5 | 4 | 15.0 | 0.39 | 0.50 |
| TRANSITION ZONE | 2 | 14 | 6.8 | 0.05 | 0.14 |
| | 3 | 154 | 10.8 | 0.38 | 0.38 |
| | 4 | 44 | 12.4 | 0.31 | 0.34 |
| | 5 | 20 | 13.0 | 0.29 | 0.35 |

Table 5.12 The expected probability of flowering calculated by the logistic regression model, based on mean rosette diameter $\bar{x}$. Observed proportions flowering and sample size n are also presented.

with age seen in Figure 5.4 was present in the observed proportions. In the slack, the actual proportions flowering in the older age classes were higher than expected, and no relationship between probability of flowering and age appears supported in the actual data for this habitat (but note the small sample sizes). In the transition zone expected and observed values agreed closely, with a similar proportion flowering in each age class.

5.3.5. Duration of the juvenile phase

Expected probabilities of transition into each age class as a juvenile plant are shown in Table 5.13 along with the observed proportions. These probabilities are affected by both survival and flowering, and were higher in general in the transition zone and dune ridge than in the slack. Table 5.13 also shows the proportion of the starting population expected and observed to be alive in the juvenile phase in each age class. Again plants in the transition zone and dune ridge had higher probabilities than slack plants. The probabilities of remaining in the juvenile phase conditional on survival indicate that transition zone plants had the highest probability of remaining juvenile, given survival, after Age 3.

A smaller proportion of plants remaining alive at a given age flowered in the transition zone than in the dune ridge and slack despite earlier initial flowering in the transition zone. By Age 3, the proportion remaining juvenile was already smaller in the dune ridge (0.35) than in the transition zone (0.53). At Age 3, juvenile plants in the transition zone and slack constitute the same proportion of surviving plants, but by Age 4, more of the plants remaining alive had flowered in the slack than in the transition

| HABITAT | TO AGE | PROBABILITY OF TRANSITION TO NEXT AGE CLASS | | REMAINING JUVENILE -CUM. | | REMAINING JUVENILE -COND. | |
|---|---|---|---|---|---|---|---|
| | | EXP. | OBS. | EXP. | OBS. | EXP. | OBS. |
| DUNE RIDGE | 2 | 0.87 | 0.79 | 0.43 | 0.39 | 0.96 | 1.00 |
| | 3 | 0.77 | 0.76 | 0.33 | 0.29 | 0.33 | 0.35 |
| | 4 | 0.19 | 0.22 | 0.06 | 0.06 | 0.16 | 0.21 |
| | 5 | 0.32 | 0.40 | 0.02 | 0.03 | 0.08 | 0.14 |
| SLACK | 2 | 0.72 | 0.40 | 0.19 | 0.11 | 0.94 | 1.00 |
| | 3 | 0.53 | 0.54 | 0.10 | 0.06 | 0.42 | 0.52 |
| | 4 | 0.14 | 0.25 | 0.01 | 0.02 | 0.27 | 0.24 |
| | 5 | 0.33 | 0.31 | 0.00 | 0.00 | 0.16 | 0.12 |
| TRANSITION ZONE | 2 | 0.83 | 1.00 | 0.40 | 0.48 | 0.95 | 0.86 |
| | 3 | 0.67 | 0.62 | 0.27 | 0.30 | 0.59 | 0.53 |
| | 4 | 0.27 | 0.24 | 0.07 | 0.07 | 0.41 | 0.35 |
| | 5 | 0.49 | 0.44 | 0.04 | 0.03 | 0.29 | 0.23 |

Table 5.13 The expected probability (EXP.) of transition of a juvenile plant from Age x-1 to Age x, the cumulative probability of remaining juvenile (CUM.) and the cumulative probability of remaining juvenile conditional on survival (COND.). The observed proportion (OBS.) in each class is also presented.

zone. Though some plants flowered at a younger age in the transition zone, a large proportion delayed flowering compared to the dune ridge and slack.

5.3.6. Survival and flowering in common garden conditions

The full results of the reciprocal transplant-replant experiment are presented in Appendix IV. Of the plants transplanted back to Pinery, none attempted flowering in 1980. There was very high overwinter mortality on the high beach, both in plants originating in the transition zone (92%) and those from the high beach (79%). The four plants which remained alive until 1981 attempted flowering that year, though the proportion successfully completing flowering was low (50%). Overwinter mortality in plants transplanted into the transition zone was much lower than in the high beach (17% of those originating in the transition zone, 23% of those from the high beach). Most of those which escaped overwinter or midseason mortality attempted flowering in 1981 (80% from the transition zone, 75% from the high beach) but again only 50% of the plants from both habitats successfully completed flowering. The other 50% died overwinter. The two plants from each habitat which remained juvenile in 1981 survived overwinter. Both plants from the high beach and one from the transition zone flowered the following year.

At Labatt Field Station (Appendix IV) one plant each from the high beach, dune ridge and slack flowered in 1980. All these plants had sibs which flowered in the same year in the greenhouse, indicating possibly a readiness of the mother plant to flower which was passed on to second generation cuttings.

Spring flooding in 1981 caused heavy mortality at the field station. All of the plants which survived overwinter and midseason mortality flowered in 1981.

In the greenhouse (Appendix IV) survival to the flowering stage was very high, ranging from 73% in high beach plants to 92% in transition zone plants. Two plants (one each from the dune ridge and high beach) died while attempting flowering. Some plants flowered in the fall of 1980, some of which were sibs of those that flowered at Labatt Field Station in 1980. Initiation of first flowering occurred throughout the experimental period, irrespective of daylength.

The fate of surviving individuals in the greenhouse is presented in Table 5.14. The number of plants which remained juvenile until the termination of the study in the transition zone sample was significantly higher than in the slack sample (Fisher's Exact test $p = 0.02$) but not significantly different from the number in the dune ridge ($p = 0.15$).

## 5.4 Discussion

The skewness apparent in the rosette diameter distributions of *A. campestris* agrees with findings from other plant populations of all growth forms (see Harper 1977, Harzo and Sarukhan 1984 for reviews). The initial decrease in skewness and subsequent stabilization over the season concur with White and Harper's (1970) predictions. They suggested that skewness should decrease and then stabilize as size-dependent mortality reduces the number of small individuals in a population. Obeid, Machin and Harper (1967)

| | DUNE RIDGE | SLACK | TRANSITION ZONE |
|---|---|---|---|
| FLOWERED 1980 | 2 | 4 | 2 |
| FLOWERED 1981 | 4 | 5 | 2 |
| FLOWERED 1982 | 1 | 2 | 1 |
| REMAINED JUVENILE | 2 | 1 | 7 |

Table 5.14 Fate of cloned plants growing under uniform conditions in the U.W.O. greenhouse. The number of plants from each habitat that flowered in 1980, 1981 or 1982, or remained juvenile throughout the study period. The table does not include those plants that died before flowering.

ascribe skewness to differences in seed size, soil microtopography, microclimatology and genetic differences magnified through time and density. Crawley (1983) suggested that a skewed distribution is an expected result of an exponential growth rate acting on an initially normal distribution. Weiner and Solbrig (1984) point out the fallacy of using skewness statistics as measures of the hierarchical structure of a population, since no account is taken of differences in means and variances. Thus skewness in a population with a mean of 100 and one with a mean of 10, but with equal variances, will have vastly different meaning if skewness is seen as a measure of unequal resource utilization within a population.

The development of bimodality has been interpreted as being the result of a few large plants having a positive growth rate and a large number of small plants having a growth rate close to zero (Ford 1975). Rabinowitz (1979) found that bimodality occurred most frequently in low density populations, and concluded that in high density stands growth of all plants was suppressed. Bimodality in this study was seen only in the slack at the end of the growing season. Of the three habitats, the slack had the highest mean density, but also the largest associated variance; ie. most plants grow in low density conditions but some grow in very high densities. Since vegetation is sparser in the slack than elsewhere, bimodality may also reflect a lack of interspecific competition in this habitat. If growth rates are bimodal, then the prolonged growth period in the slack may have allowed a clearer expression of the consequences of this. Recruitment and mortality patterns reported in Chapter 4 produce an unstable age structure in this

habitat, and therefore bimodality may be a result of a lack of plants in the middle age groups since size is related to age.

Rapid growth occurred in all habitats at the beginning of the season. Boorman (1982) found similar results for sand dune annuals, which did most of their growing between the time the soil warmed up and the onset of midsummer drought. *Salicornia europaea* growing in an upper marshland subject to late season hypersalinity had a high growth rate only at the beginning of the season (Jefferies, Davy and Rudmick 1979). In contrast, plants in the lower marshland, with no seasonal changes in salinity, grew throughout the season. Plants in the transition zone virtually stopped growing after an initial spurt, probably due to competition with other species in this heavily vegetated habitat. Increased density of either interspecific and intraspecific populations reduced plant size in sand dune annuals (Pemadasa and Lovell 1974). Hicks (1938) found growth in *A. caudata* (*sic*) limited by both available nitrogen and light intensity. Although the transition zone, with higher organic matter content in the soil, may have more absolute nitrogen than the other habitats, there are also more plants competing for that nitrogen, and thus less may be available. "Forest" plants contained less nitrogen than beach plants in Hicks' (1938) study. As shrubs and trees leaf out, light may be reduced as the season progresses. The reduction in proportional rosette diameter increase in the dune ridge during the mid-season period may be caused by light interception by shrubs. Growth in the slack was apparently unaffected by these factors. Reduced rosette diameter increase in the late season was expected, as this is the time when carbohydrate reserves are built up in the tap root for overwinter survival

and the next season's initial growth.

Age and initial size both contributed to the final size of an individual in the *A. campestris* population, but there was no evidence that growth rates as measured by increased rosette diameter differed among ages or size classes. Boorman (1982) found that growth rates of sand dune biennials varied. *Cynoglossum officinale* occurred in disturbed areas and had a relatively low growth rate compared to *Lactuca virosa* which grew under competitive conditions. Plants in the dune ridge appear to have a more rapid annual growth rate than those in the slack and the transition zone, since the mean rosette diameter even when adjusted for initial size was larger than in the other habitats. Grime and Hunt (1975) identify high $R_{max}$ (maximum potential growth rate) with both competitive and ruderal strategies, but note that even in the ruderal strategy, high $R_{max}$ may be an adaptation to competition in the early stages of colonization. It is impossible to make a direct comparison between $R_{max}$ determined among species under laboratory conditions and behaviour among conspecific populations in the field. However, of the three habitats studied, *Artemisia campestris* attains its highest growth rate under moderately competitive conditions (the dune ridge). Growth is suppressed by high levels of competition (transition zone) as well as under conditions disturbed by humans and abiotic factors, or stressful enough that other species cannot grow (slack).

The covariance of multiple stems and plant size is twofold. First, the use of the term "diameter" implies a circular measurement. In some multiple stemmed plants, rosettes were formed in a more linear fashion. Measurement

of a single rosette diameter, across the entire plant, overestimated the photosynthetic surface being evaluated. Secondly, multiple stems develop only rarely in young plants. Since size covaries with age it is not surprising that multiple stems should be correlated with size.

In the prediction of the presence of multiple stems, tissue destruction was the single most important factor in the field. Hartnett and Abrahamson (1979) found similar results in *Solidago canadensis* populations. In *A. campestris* populations investigated here, older larger plants were most susceptible, either because their large size attracted herbivores more readily (Solbrig, Newell and Kincaid 1980), or because of increased time of exposure. The lack of visible damage in Age 5 multistemmed plants may be the result of damage occurring prior to the recording period and no longer visible. Similarly, the fact that the presence of damaged tissue was not always associated with multiple stems may be due to the death of multiple stems, damage to tissue other than the meristem or lack of time for development of multiple stems. Even though the relationship between damage and multiple stems is strong, there may be other factors affecting development such as genotypic propensity or herbivory occurring at a level not examined, in the root or internally (Crawley 1983). Qualitative observation on plants grown in the greenhouse and at Labatt Field Station suggest that all plants have the potential to produce multiple stems, unrelated to damage.

Plants in the slack and transition zone were far more susceptible to herbivore attack than those on the dune ridge. The lower wind velocity, allowing easier settling of insects on the plants, relative floristic richness and older age structure in the transition zone may provide a partial

explanation. Higher population densities in the slack may increase the probability of infestation of neighbouring plants.

Werner (1975), Gross (1980), and Gross and Werner (1983) found that survival increased with increasing rosette size although the shapes of the linear or negative exponential functions varied among species. Survivorship in *A. campestris* also generally increased with increasing rosette diameter, particularly in the second year. However, the relationship between survival and rosette diameter was reversed in the oldest age group studied. Larger plants actually had a higher expected mortality rate. This must be interpreted cautiously due to small sample sizes, but it suggests that some disruption to the floral initiation process occurs, preventing flowering and eventually killing the plant. Examination of the roots of these large old plants would possibly be informative.

Survivorship decreased with age, with the exception of the Age 4 to 5 period. Possibly this was due to a process of culling weaker plants in the first years of life, leaving only the strong or plants in microenvironmentally safe conditions. More probably it is a reflection of the confounding of age and year discussed in Section 5.2.4. Age 4 plants were sampled in 1979 for prediction of fate in 1980. The 1979-80 winter was characterized by abnormally little snow, a long January thaw, and a cold dry spring (Pinery Provincial Park Meteorological Station). *Artemisia campestris* is one of the earliest species to grow in the sand dune community and the warm weather in January probably initiated early plant growth. Little protective snow cover combined with a cold dry spring may have resulted in exceptionally high mortality.

The rosette diameter of *A. campestris* was highly significant in predicting flowering. Above the critical diameter, the probability of flowering increased with rosette size. The results agree with those of Werner (1975), Baskin and Baskin (1979a, b), Gross (1980), Hirose and Kachi (1982) and Gross and Werner (1983) who showed that in several monocarpic perennials, a critical rosette diameter must be reached before flowering can occur. Kelly (1985b) suggests that this is characteristic of facultative biennials.

RD50 is a more stable reflection of the rosette diameter necessary for flowering than the minimum rosette diameter since it is based on more than a single value and hence is not as subject to the possible aberrant behaviour of a single individual. The usefulness of the calculated RD50 is strongly affected by the adequacy of the model from which it is derived. If the fit of the data is good the RD50 may be a more useful summarizer of the flowering of plants in specific habitats. It does not, however, supersede the value of the minimum rosette diameter in absolute biological description of the behaviour of a species. It is suggested that the values be used in conjunction with one another.

The trend towards larger critical size for flowering on the dune ridge as opposed to the transition zone may be due to improved soil and microenvironmental conditions in the older habitat. Hirose and Kachi (1982) showed that the critical size of four sand dune species varied inversely with the gradient of soil fertility in the dune system. If the fertility of a habitat is related to its floristic richness (competition), and maximum growth rate is limited by this, then selection may operate to promote

flowering at smaller sizes in fertile environments. Similarly, if the number of capitula produced the following year is sufficiently increased by a year's further growth (Caswell and Werner 1978; Silvertown 1983; Kelly 1985a), delayed reproduction and flowering at larger sizes may be selected for in infertile habitats. Van der Meijden and van der Waals-Kooi (1979) found that delayed flowering in *Senecio jacobaea* increased the number of capitula produced the following season. This suggests that some cue for flowering in addition to carbohydrate balance may exist (Sachs and Hackett 1983) though maternal influence cannot be discounted.

An increase in soil nutrient levels resulted in a lowering of age at reproduction in one system investigated (Hirose and Kachi 1982). However, decreased availability of space (Ross and Harper 1972), greater species diversity (Baldwin and Maun 1983) and canopy cover (Werner 1975, 1977), all associated with high soil nutrient levels, may delay the attainment of critical diameter. Because the growth rate is slower in general in the transition zone population, the time to reach critical size is often longer than in the other habitats, even though the critical size is smaller. Since the probability of survival at later ages is high in the transition zone and the probability of flowering at any age is relatively low, plants in the transition zone have an overall higher probability of remaining juvenile for longer periods.

The most common age for flowering is Age 3, particularly in the dune ridge. Plants flowering in this age group were smaller than those which flowered later. This suggests a limit to increases in fecundity through delay in reproduction. Plants which flowered at Age 4 and Age 5 may have attained

a size large enough for flowering too late in the previous season to flower at Age 3. That older plants are less likely to flower regardless of size is harder to explain, unless a disruption to the floral initiation system is again postulated.

## 5.5 Summary

1. Rosette diameter distributions are right-skewed, with skewness decreasing and stabilizing over the season.

2. The most rapid growth of rosette diameter occurs at the beginning of the season. Little increase in rosette diameter occurs after that in the transition zone. A reduction in rosette diameter increase occurs in the dune ridge in the midseason period, but not until the final period in the slack.

3. Overall rate of increase in rosette size is highest in the dune ridge.

4. Plants in the dune ridge are most likely to be single-stemmed. Tissue damage occurs least frequently in this habitat. The multiple stemmed state is highly associated with visible tissue damage.

5. Survival is increased by larger rosette size, and decreased by age. Survival is lowest in the slack and highest in the dune ridge.

6. Plants flower at smaller diameters in the slack and transition zone than in the dune ridge.

Older plants in the dune ridge are less likely to flower than younger ones after Age 3. The optimal age for flowering is Age 3, though in the transition zone some plants were observed to flower at Age 2.

7. The juvenile phase is longest in the transition zone and shortest in the dune ridge.

# CHAPTER 6

# REPRODUCTION

## 6.1 Introduction

The approach to the reproductive phase of *Artemisia campestris* taken in this study is necessarily multi-faceted. For the small proportion of the total population which reach the flowering stage, many factors influence flowering success and fecundity, and these factors are often interrelated. Among the factors investigated here are survival during and after flowering, size of the plant before and during flowering, insect damage, and fertilization success. In a facultative polycarp, the number of flowering events, and the genetic determination of this, also affect an individual's actual and potential fecundity. Flowering schedules not only affect fertilization success within populations but also reflect the degree of potential gene flow between (possibly differentiating) populations.

Temporal isolation in flowering time is an effective method of reproductive isolation between populations (Stebbins 1950; Mayr 1963; McNeilly and Antonovics 1967). Flowering schedules may be under direct genetic control (McNeilly and Antonovics 1967; Kiang and Hamrick 1978), or contain a strong phenotypic component (Augspurger 1981; Lee and Hamrick

1983). Differences in timing of anthesis between conspecific populations growing in different habitats have been related to the temperature and moisture content of soil (McNeilly and Antonovics 1967), density (Palmblad 1968; Sterk 1975) and resource limitation (Hickman 1975). If flowering schedules differ or vary in length among populations, then the environment in which seeds mature will also differ. Ripening conditions influence seed weight and germination rates (Smith 1973; Gutterman 1977) and seedling growth characteristics (Stearns 1960; Rowe 1964; Schaal 1984; Alexander and Wulff 1985).

Within a population, temporally isolated individuals show reduced seed set due to lowered pollen availability (Schemske 1977; Augspurger 1981). Pollination success in anemophilous species is also affected by plant characteristics such as height of the plant, receptive stigmatic surface area and pollen grain size and longevity (Whitehead 1969; Primack 1978; Faegri and van der Pijl 1979). Other factors are density of the population and height of the surrounding vegetation (Whitehead 1969; Faegri and van der Pijl 1979). Abiotic factors influencing pollination success are wind velocity and direction, and rainfall patterns (Whitehead 1969). Pollen flow as a method of gene exchange between populations is a function of distance between populations (Levin and Kerster 1974; Hamrick 1982; Levin 1983).

Most of the seeds produced in plant populations may be contributed by only a few individuals (Leverich and Levin 1979; Schaal 1980). Fecundity is frequently size-related (van der Meijden and van der Waals-Kooi 1979; Fowler and Antonovics 1981; Newell, Solbrig and Kincaid 1981; Solbrig 1981). Density may either depress (Palmblad 1968; Keddy 1981) or increase (Klemow

and Raynal 1981) seed output. Herbivory generally decreases fecundity (Cameron 1935; Holt 1972; Hartnett and Abrahamson 1979; Bentley, Whittaker and Malloch 1980) or delays flowering to the following year (Cameron 1935; van der Meijden and van der Waals-Kooi 1979). Herbivory can also affect seed weight (Maun and Cavers 1971; Bentley, Whittaker and Malloch 1980; Marshall, Levin and Fowler 1985).

Data on survival between initiation and completion of flowering are relatively scarce, since most are subsumed within whole-population survivorship curves. The fate of plants in which the floral meristem dies may be either death of the whole plant at a later date or flowering during some subsequent year (Cameron 1935; van der Meijden and van der Waals-Kooi 1979). In weakly polycarpic species, flowering a second or third time has been related to lowered competitive stress in *Plantago major* (Hawthorn and Cavers 1976) but to increased competition in populations of *Anthyllis vulneraria* (Sterk 1975).

The following questions will be addressed in this chapter:

1. What are the phenological stages in flowering of *Artemisia campestris*? Do these differ temporally or in duration among habitats?

2. Are there differences in fecundity among habitats and years? Is fecundity related to size and/or insect damage?

3. Are there differences in seed mass among habitats?

4. What proportion of the field population

attempting flowering is successful? Does this differ among habitats? What is the degree of polycarpy in each habitat? Are differences replicable under uniform conditions?

5. Are there quantifiable differences between plants which survive flowering and those that die after the first flowering event?

## 6.2 Methods

### 6.2.1. General methods

Plants mapped and tagged in the main study (see Chapter 3 for details) were observed for elongation of the flowering stem (bolting) during the summers of 1979 and 1980. The sample was augmented to include at least 25 flowering plants per habitat in August 1979, using the random coordinate method described in Chapter 3. Eight plants were added in the slack, four in the transition zone and none in the dune ridge by this method. Twenty-five additional flowering plants were added to the study in 1980 to allow destructive harvesting of sampled individuals without interference with the observation of fate during the following growing season. Added plants were tagged and numbered. Samples were small due to the labour intensive nature of the study and the importance of not destroying the population's seed source for the following season.

### 6.2.2. Phenology

Stages of flowering were stipulated following observations in 1978 and are presented in Table 6.1. Phenological monitoring took place over two-

1. BOLTING-elongation of cells formed by the apical meristem following floral induction

2. BUDS EMERGING-capitula apparent but not fully developed

3. BUD-capitula fully developed but unopened

4. FLOWERS OPEN-capitula opened but anthers not extruded

5. ANTHESIS 1-anthers extruded from the capitula

6. ANTHESIS 2-anthers extruded from some capitula; stigmatic surface receptive in some

7. ANTHESIS 3-pollen dispersed; capitula remain open; stigmatic surfaces receptive

8. POST-ANTHESIS CLOSURE-capitula closed

9. DEHISCENCE-capitula reopened; seed dispersal can occur

Table 6.1 Definition of phenological stages during flowering of *Artemisia campestris*.

day periods starting August 19, August 29, September 5, September 12 and September 28 in 1979, and August 11, August 20, August 28, September 3, September 11 and September 28 in 1980. On each observation date, the phenological stage was recorded. In 1979, stages of the top one-third, middle third and lower third of each plant were determined by eye and recorded.

6.2.3. Seed production

Marked plants were harvested at seed maturity in the months of October and November in all 3 years. Seed maturity was judged at weekly intervals by opening capitula in the field and observing colour (mature seeds are black) and fullness. Flowering stems were harvested just above ground level. The plants were airdried and stored in paper bags in a drying cabinet at the University of Western Ontario. Twenty capitula from all parts of the plant were collected and stored separately in paper envelopes. The number of mature seeds per capitulum was counted in each of the 20 capitula. The number of capitula on each plant was then counted manually. Total seed production was estimated by multiplying the number of seeds per capitulum by the total number of capitula. In the 1981 sample, damage to the capitula and seeds was also noted. Deformed (shrivelled) and underdeveloped seeds, as well as mature ones, were counted.

6.2.3.1. Height variables

Two height measurements were made, total height and height of the inflorescence. Total height was measured from the ground to the top of the plant. Inflorescence height was defined as the portion of the stem on

which capitula, or branches with capitula, occurred (Figure 2.1). In the analyses, total height and inflorescence height were summed over all flowering stems on a plant. Average height and average inflorescence height were obtained by dividing the appropriate quantities by the number of flowering stems.

6.2.3.2. Number of capitula per plant

An analysis of covariance was used to test differences in mean capitula number per plant among years and habitats, adjusted for inflorescence height and damage to the whole plant. The continuous variables were $\log_e$ transformed. Damage was scored 1 (present) or 0 (absent). The analysis was followed by a GT2 comparison of means test for unequal sample sizes (Sokal and Rohlf 1981).

6.2.3.3. Seed number per capitulum

An analysis of variance was performed on square-root transformed seed production per capitulum among habitats and years. Examination of correlations between this variable and size variables revealed no relationships. The analysis was followed by a GT2 comparison of means tests for unequal sample sizes (Sokal and Rohlf 1981).

The maximum number of seeds observed per capitulum was eight. This was taken as a (local) maximum reproductive potential. The total reproductive potential for an individual plant was then calculated as (8 × the number of capitula).

6.2.3.4. The effect of damage

It was thought that the total number of seeds per capitulum would be related to the amount of damage to the capitulum. A capitulum was considered damaged if part of it had been eaten, if there was any evidence of insect presence (frass, cocoons) or if an insect was present in the capitulum. Damage to the capitulum was scored 1 or 0. Thus the maximum theoretical score (all capitula affected) was 20. The correlation between total number of seeds and number of capitula affected was calculated. A G test for independence of habitat and damage was performed. Because the number of plants in the higher damage classes was small, plants were classified as (1) not damaged, (2) damage to 1 capitula, and (3) damage to more than 1 capitula for this analysis.

6.2.3.5. Harvest date

The harvest date reflects the time to maturity of the seeds, and the conditions under which they ripen. Means and variances of seed production per plant at each harvest date were calculated by habitat.

6.2.3.6. Fall rosette diameter

The usefulness of fall rosette diameter as a predictor of the following year's reproductive output was determined through the regression of height variables, capitulum number and seed production on fall rosette diameter.

6.2.4. Seed rain

The number of reproductive plants in each plot was counted in 1980 and 1981. Seed rain per square metre was estimated by multiplying the mean number of reproductive plants by the mean number of seeds per plant in each habitat. The geometric rather than the arithmetic mean of seed number was used to more accurately reflect the distribution of seed number per plant.

6.2.5. Seed mass

Ten mature seeds from each plant harvested in 1980 were weighed using a Mettler H12 balance, and mean seed mass determined for each plant. Differences in seed mass among habitats were tested using a one-way analysis of variance, followed by a Tukey-Kramer comparison of means test for unequal sample sizes. Correlations between seed number and seed mass were calculated.

6.2.6. Fate of individuals

6.2.6.1. In the field

Fate (survival, death, loss of the floral meristem without death of the plant) was observed on phenological observation dates, as well as at least once the following May to determine postflowering survival and further flowering events.

6.2.6.2. In common garden conditions

See Chapter 3 for details. The number and pattern of flowering events of plants grown in the U.W.O. greenhouse and at Labatt Field Station were recorded from June 1980 to December 1982. A G test for independence (Sokal and Rohlf 1981) was performed on postflowering survival among habitats. Data on flowering success from the reciprocal transplant-replant experiment was scant and is not presented here. See Appendix IV for full results.

6.2.7. Postflowering survival and height during flowering

Only total height, rather than total height and inflorescence height, of the plant was measured in 1978. Because the sample size of plants which survived flowering was small and included plants which flowered in 1978, total height of the plant at flowering was used as a measure of reproductive potential. Plants in the habitats in which postflowering survival was observed were categorized by fate: (1) death after flowering, (2) postflowering vegetative survival, and (3) more than one flowering event. Means and variances of total height in each group were calculated. Variances between the groups in the dune ridge were similar, and a t-test for unequal sample sizes was performed. Variances in the transition zone were dissimilar and unaided by transformation; therefore the means were tested using the Games and Howell method for more than two samples with heterogeneous variances (Sokal and Rohlf 1981).

## 6.3 Results

### 6.3.1. Phenology

Nine stages in the flowering process were stipulated (Table 6.1). Bolting occurred in mid-June of both years. The number of plants in each phase during the main phenological study is presented in Tables 6.2a and 6.2b. Where more than one phase was present within a single plant, the plant was considered to be in the most advanced stage.

In the dune ridge in 1979 32% of the flowering plants had reached Stage 5, anther extrusion, by August 19 (Table 6.2a). All other plants were less mature. By the end of August the majority of plants were already in Stage 7, stigmatic receptivity. Thus the peak of anthesis (Stage 5) occurred during the fourth week in August. By the end of the first week in September, most inflorescences were closed and dehiscence began in the following week. Most of the seeds did not dehisce until after the end of September.

Anthesis occurred earlier in 1980 than in 1979 (Table 6.2b), peaking at approximately the third week of August. By the end of August 60% of the plants had at least some capitula already closed. Thus the duration of phases showed similar patterns between years, with plants in 1980 approximately one week earlier than in 1979. Dehiscence appeared comparatively delayed in 1980.

The initial stages of the flowering process occurred contemporaneously in the slack and the dune ridge in both years (Table 6.2). However, Stage 5 (anther extrusion) lasted longer in the slack, and the overlap between

AUGUST 1979

| | 8/19 | | | 8/29 | | |
|---|---|---|---|---|---|---|
| PHASE | DR | SL | TZ | DR | SL | TZ |
| 1 | | | 1 | | | |
| 2 | 2 | 1 | 2 | | | 1 |
| 3 | 9 | 10 | 20 | | | 3 |
| 4 | 6 | 6 | 2 | 2 | 2 | 3 |
| 5 | 8 | 8 | | 1 | 7 | 18 |
| 6 | | | | 4 | 12 | |
| 7 | | | | 17 | 4 | |
| 8 | | | | | | |
| 9 | | | | | | |
| DEAD | | | | | | |

SEPTEMBER 1979

| | 9/5 | | | 9/12 | | | 9/30 | | |
|---|---|---|---|---|---|---|---|---|---|
| PHASE | DR | SL | TZ | DR | SL | TZ | DR | SL | TZ |
| 1 | | | | | | | | | |
| 2 | | | | | | | | | |
| 3 | | | 1 | | | 1 | | | |
| 4 | | | 1 | | | | | | |
| 5 | 1 | 1 | 6 | | | 2 | | | |
| 6 | 2 | 5 | 16 | 1 | 1 | 8 | | | 3 |
| 7 | 3 | 10 | 1 | | 7 | 11 | | 3 | 9 |
| 8 | 17 | 9 | | 19 | 26 | 3 | 16 | 14 | 10 |
| 9 | | | | 3 | 1 | | 7 | 3 | 3 |
| DEAD | 2 | | | 2 | | | 2 | | |

Table 6.2a Number of plants in each phase of flowering in August and September 1979 in the dune ridge, slack and transition zone. Where more than one phase was observed on an individual plant, the plant was treated as being in the most advanced phase. 1 - Bolting; 2 - Buds emerging; 3 - Bud; 4 - Flowers open. 5 - Anthesis 1; 6 - Anthesis 2; 7 - Anthesis 3; 8 - Postanthesis closure; 9 - Dehiscence. See Table 6.1 for definitions of the phases.

AUGUST 1980

| | 8/11 | | | 8/20 | | | 8/28 | | |
|---|---|---|---|---|---|---|---|---|---|
| PHASE | DR | SL | TZ | DR | SL | TZ | DR | SL | TZ |
| 1 | | | 3 | | | 2 | | | 2 |
| 2 | | | 6 | | | 6 | | | 0 |
| 3 | 7 | 9 | 9 | 5 | 6 | 31 | 2 | | 5 |
| 4 | 1 | 2 | | 10 | 11 | 3 | | | 6 |
| 5 | 5 | 3 | | 24 | 25 | 6 | 1 | 9 | 30 |
| 6 | | | | | 1 | | 1 | 7 | 4 |
| 7 | | | | 4 | 1 | | 13 | 9 | 1 |
| 8 | | | | | | | 26 | 19 | |
| 9 | | | | | | | | | |
| DEAD | | | | | | | | | |

SEPTEMBER 1980

| | 9/3 | | | 9/11 | | | 9/23 | | |
|---|---|---|---|---|---|---|---|---|---|
| PHASE | DR | SL | TZ | DR | SL | TZ | DR | SL | TZ |
| 1 | | | 2 | | | 1 | | | 1 |
| 2 | | | | | | | | | |
| 3 | | | 1 | | | | | | |
| 4 | | | | | | | | | |
| 5 | | | 18 | | | 6 | | | |
| 6 | | 6 | 22 | | | 27 | | | |
| 7 | | 3 | 6 | | 1 | 4 | | 1 | 27 |
| 8 | 41 | 35 | | 41 | 43 | 8 | 37 | 38 | 14 |
| 9 | | | | | | 1 | 4 | 5 | 4 |
| DEAD | 2 | | | 2 | | 2 | 2 | | 3 |

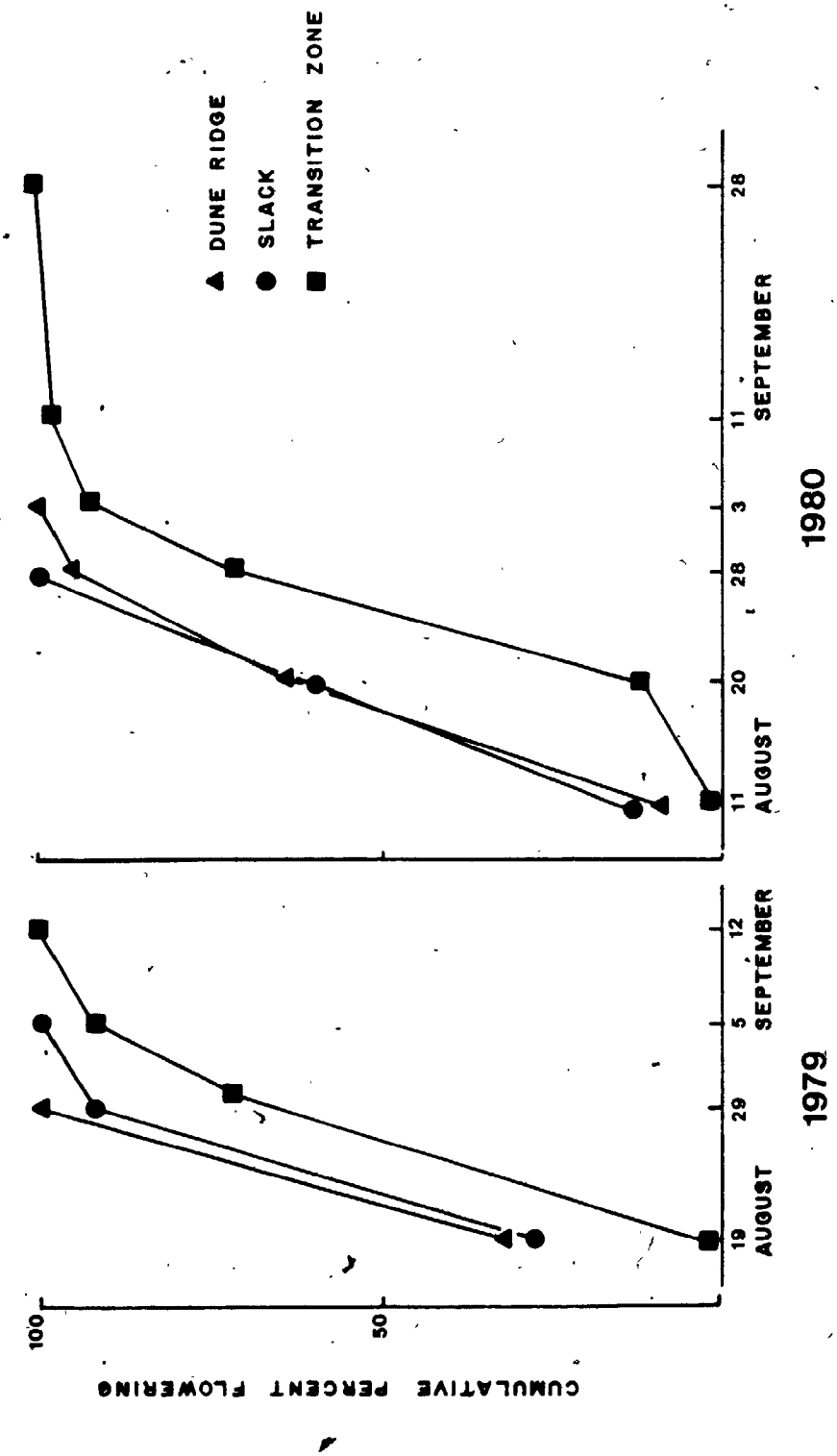
Table 6.2b Number of plants in each flowering phase in August and September 1980 in the dune ridge, slack and transition zone. Where more than one phase was observed an individual plant, the plant was treated as being in the most advanced phase. See Table 6.1 for definitions of the phases.

anther extrusion and stigmatic receptivity (Stage 6) was a more marked phase in the slack than in the dune ridge. Thus pollen availability and stigmatic receptivity from plants in this habitat were both more prolonged. As in the dune ridge, flowering occurred approximately one week earlier in 1980 than in 1979.

Anthesis did not occur in the transition zone until the final week of August in 1979. By the first week in September, most plants had lost at least some of their pollen and were stigmatically receptive. The period of overlap of anther extrusion and stigmatic receptivity was more prolonged than in the other habitats. By the end of September almost half were still in an active stage of flowering. In 1980, while anthesis began in the third week of August, a week earlier than in 1979, the peak occurred in the final week of August as in 1979. The joint occurrence of anther extrusion and stigmatic receptivity lasted longer in 1980 than in 1979.

Figure 6.1 depicts the cumulative percentage of the population flowering at each date in 1979 and 1980. The cumulative percentage flowering was defined as the total number which had reached Stage 5 on or before a given date. The figure shows clear temporal trends in flowering even though peak dates may have been missed. All plants that lived had flowered by the end of August in the dune ridge in 1979 and 1980, by the first week of September in the slack in both years and generally by the second week of September in the transition zone, though one plant did not begin to flower until late September in this habitat.

Figure 6.1 Cumulative percentage flowering of reproductive plants in three habitats during August and September 1979 and 1980.


DUNE RIDGE
SLACK
TRANSITION ZONE
CUMULATIVE PERCENT FLOWERING
100
50
19
29
5
12
AUGUST
SEPTEMBER
1979
11
20
28
3
11
28
AUGUST
SEPTEMBER
1980

The stages reported in Table 6.2 and Figure 6.1 indicate only the most advanced phase identified on the plant. How representative these stages were of the whole plant's activity is indicated by Table 6.3. With the exception of August 29 in the slack and dune ridge, coincident with the peak of stigmatic receptivity, plants appeared to mature as a whole; when they didn't, there was a slight trend toward early maturation on the upper third of the plant. It is possible that pollen was removed more readily from the upper third of the plant since the wind could be expected to be stronger at greater heights. No strong trends were apparent in the transition zone, though the general trend was similar to that in the other habitats.

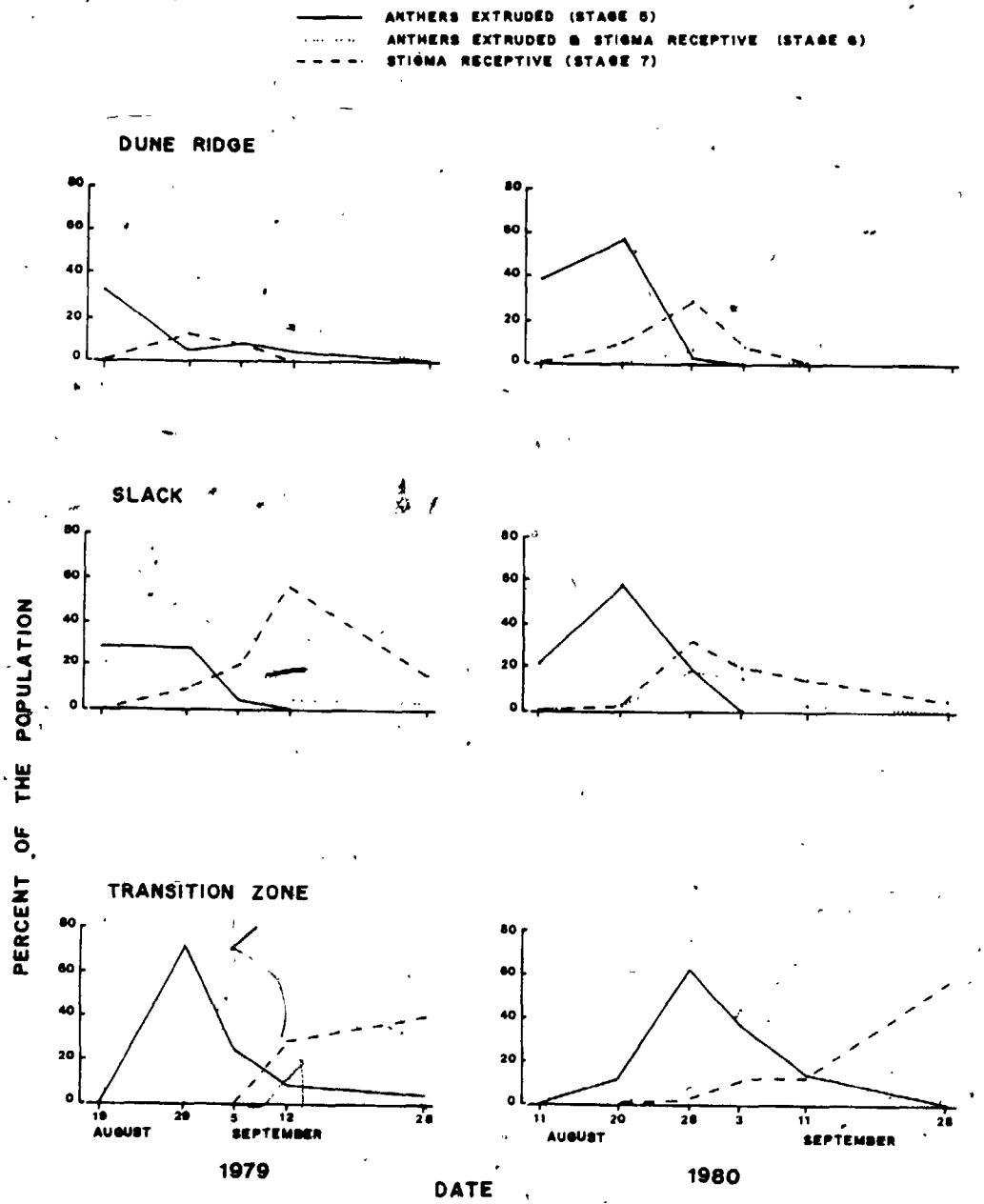
Figure 6.2 presents the proportion of the population in an active flowering stage, i.e. anthers extruded, stigma receptive or the overlap period. A plant was considered actively flowering even if a more advanced stage was also present. It should be noted that the peaks of anther extrusion in the dune ridge and slack in 1979, inferred from Table 6.2 to have occurred between observation dates, are not apparent in this figure.

Temporal trends in active flowering were similar in 1979 and 1980 (Figure 6.2). In the dune ridge, the active flowering period was earlier and shorter, and the overlap stage small. In the slack, Stages 5 and 6 were short compared to the transition zone, but Stage 7 endured until the end of the flowering period. In the transition zone, in addition to the relative lateness already noted, it is apparent that Stage 6 was much longer and that stigmatic receptivity in general lasted well beyond active flowering in the other habitats.

| | PART OF PLANT MOST ADVANCED | AUGUST 19 | AUGUST 29 | SEPTEMBER 5 | SEPTEMBER 12 | SEPTEMBER 24 |
|---|---|---|---|---|---|---|
| DUNE RIDGE | UPPER | 4 | 15 | 6 | 2 | 1 |
| | MIDDLE | 0 | 1 | 0 | 0 | 0 |
| | LOWER | 4 | 0 | 2 | 0 | 0 |
| | SIMULTANEOUS | 17 | 9 | 17 | 23 | 24 |
| SLACK | UPPER | 5 | 13 | 6 | 3 | 0 |
| | MIDDLE | 0 | 1 | 0 | 0 | 0 |
| | LOWER | 2 | 2 | 2 | 2 | 1 |
| | SIMULTANEOUS | 18 | 9 | 17 | 20 | 24 |
| TRANSITION ZONE | UPPER | 2 | 3 | 5 | 7 | 4 |
| | MIDDLE | 0 | 1 | 2 | 1 | 0 |
| | LOWER | 2 | 0 | 2 | 0 | 0 |
| | SIMULTANEOUS | 21 | 21 | 16 | 17 | 21 |

Table 6.3 Number of plants with upper, middle or lower thirds in the most advanced phase of flowering. Plants with all parts flowering simultaneously are designated "simultaneous". Data are presented for each observation date in 1979 in the dune ridge, slack and transition zone.

Figure 6.2 Percentage of the flowering population in each of three active stages of flowering in August and September 1979 and 1980.


ANTHERS EXTRUDED (STAGE 5)
ANTHERS EXTRUDED & STIGMA RECEPTIVE (STAGE 6)
STIGMA RECEPTIVE (STAGE 7)
DUNE RIDGE
SLACK
TRANSITION ZONE
PERCENT OF THE POPULATION
0
20
40
60
80
19
29
5
12
26
11
20
26
3
11
26
AUGUST
SEPTEMBER
1979
1980
DATE

When plants in the dune ridge had the highest stigmatic receptivity, plants in the transition zone were at maximum anther extrusion in both 1979 and 1980 (Figure 6.2). Overlap in flowering stages was moderately great between the slack and transition zone in 1979, but less in 1980. The coincidence between stages in the dune ridge and slack was high in both years in the initial stages, but the stigmatic receptivity stage was longer in the slack.

### 6.3.2. Seed production

The arithmetic means and 95% confidence limits derived from the $\log_e$ transformed data of seed production per plant are presented in Figure 6.3 on a semilog scale (for ease of presentation). The means ranged from 250 seeds per plant in the transition zone in 1979 to almost 2000 in the slack in 1981, and they were accompanied by very wide confidence limits. Year to year variability was apparent within habitats but the pattern remained consistent among years. Plants in the slack produced the highest number of seeds in all three years and those in the transition zone the lowest.

#### 6.3.2.1. Individual contribution to the seed population

The cumulative contribution of each (ranked) individual to the total seed population is shown in Figure 6.4 for each habitat-year combination. In each habitat 50% of the total seeds were produced by approximately 15% of the plant population. Fifty per cent of the population produced between 80 and 90% of the seeds. Thus only a few individuals in each population contributed numerically to the next generation.

Figure 6.3 Mean seed production per plant in the dune ridge, slack and transition zone in each of three years. Arithmetic means and 95% confidence limits derived from $\log_e$ transformed data are presented on a semilog scale.

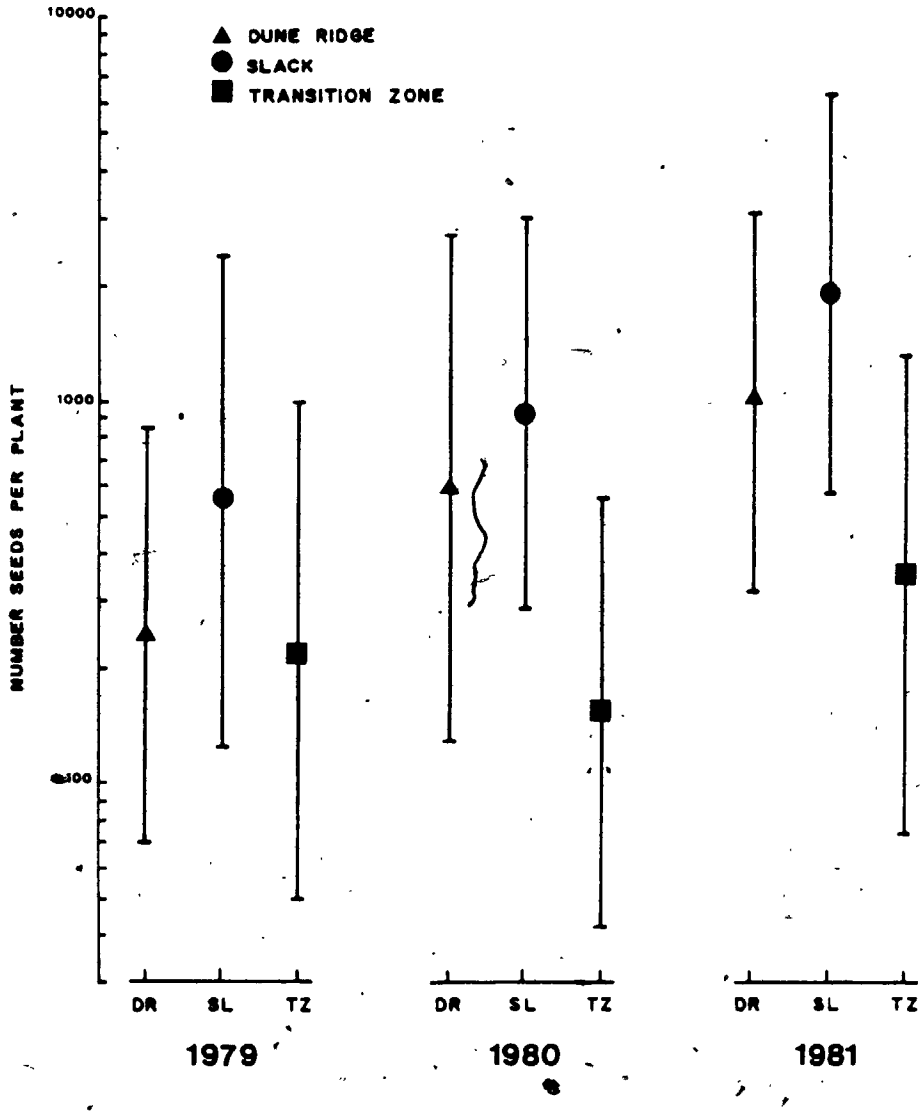
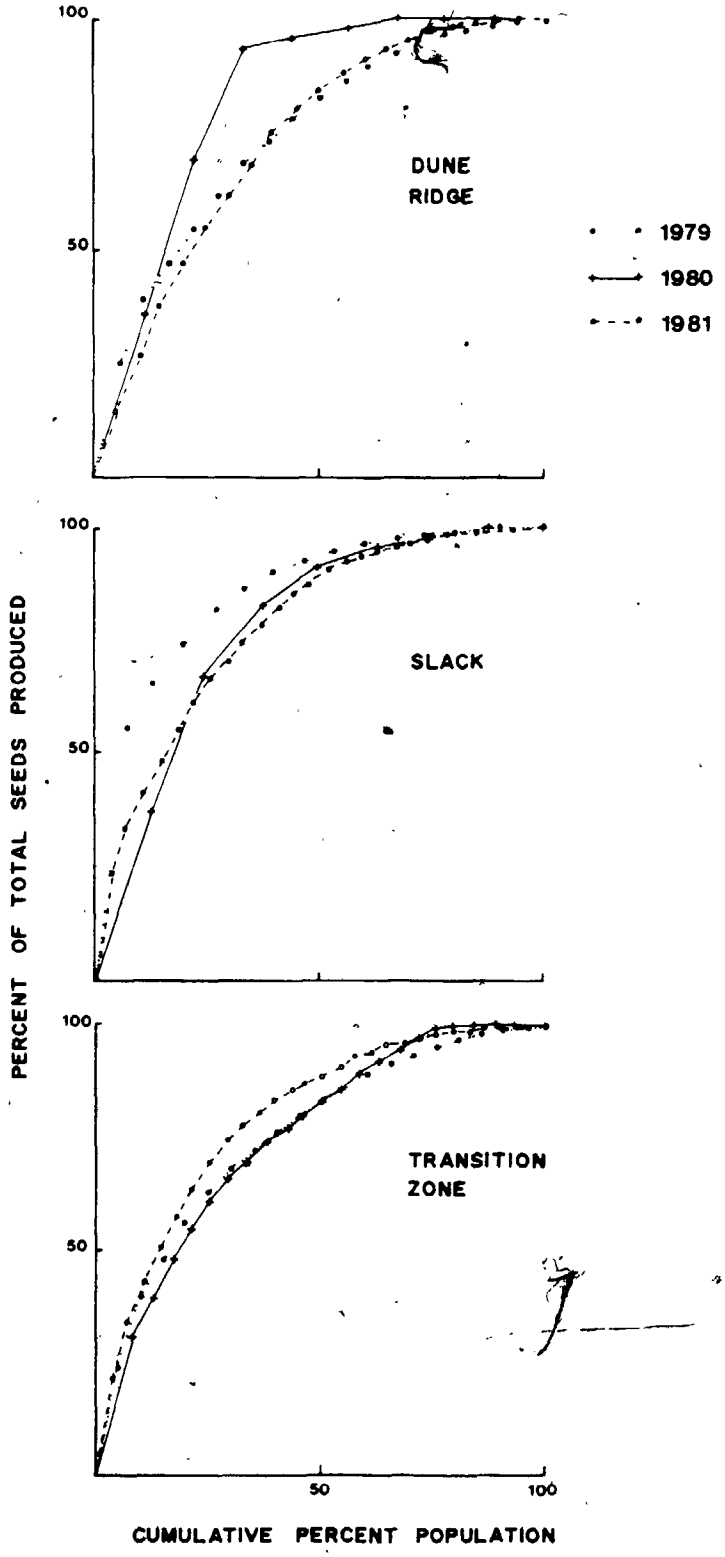

10000
1000
100
NUMBER SEEDS PER PLANT
DUNE RIDGE
SLACK
TRANSITION ZONE
DR
SL
TZ
1979
1980
1981

Figure 6.4 The percentage of seeds contributed by each individual to the total seed population, in the dune ridge, slack and transition zone over three years. Individuals were ranked from highest to lowest before accumulating.


100
50
DUNE
RIDGE
1979
1980
1981
100
50
SLACK
100
50
TRANSITION
ZONE
50
100
PERCENT OF TOTAL SEEDS PRODUCED
CUMULATIVE PERCENT POPULATION

6.3.2.2. Height

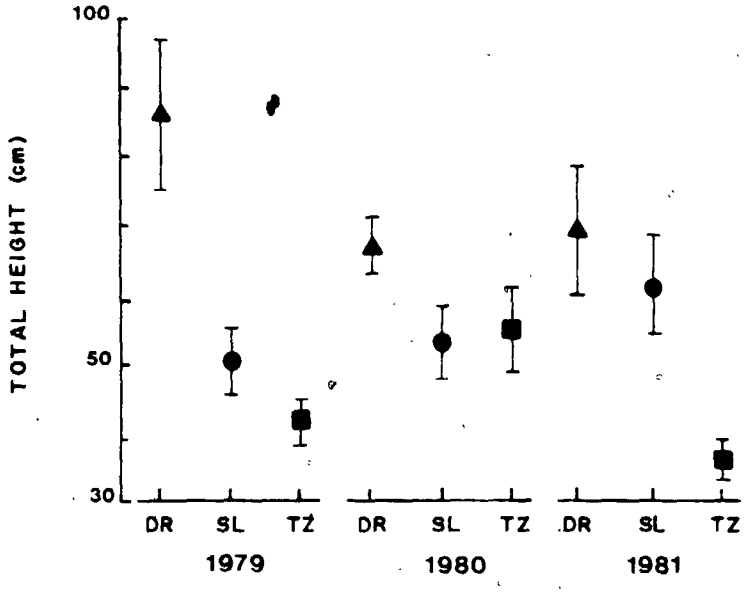
Figure 6.5 presents the means and standard errors of total height and inflorescence height. Plants from the dune ridge were taller in all three years. Slack plants were taller in 1979 and 1981 than transition zone plants, but no difference was observed in 1980. Within habitats, dune ridge plants were larger in 1979 than in the other years, with little difference between 1980 and 1981. The mean height of slack plants in 1979 and 1980 were similar, and the mean in 1981 was slightly larger. Transition zone plants were tallest in 1980, with little difference between 1979 and 1980.

Inflorescence height (Figure 6.5, lower) behaved more consistently among years, showing little within habitat variation and a constant trend. Dune ridge plants were tallest, slack plants intermediate and transition zone plants smallest in height in all three years. Total height of plants appeared to vary more than inflorescence height, both within and among habitats.

6.3.2.3. Capitulum number per plant

Number of capitula per plant (Figure 6.6) showed the same trends as the other size variables. The analysis of covariance showed no interaction between habitat and year in capitula number (Table 6.4). There was no difference among years but differences among habitats in adjusted mean capitulum number were significant. The regression of capitulum number on inflorescence height and damage was significant. Only inflorescence height was significant as a covariate. Damage to the mother plant had no effect on capitulum number. $\text{Log}_e$ transformed means, standard errors and means

Figure 6.5 Means and standard errors of total height per plant (upper), and inflorescence height per plant (lower) in the dune ridge, slack and transition zone in each of three years.


100
50
30
TOTAL HEIGHT (cm)
DR
SL
TZ
DR
SL
TZ
DR
SL
TZ
1979
1980
1981

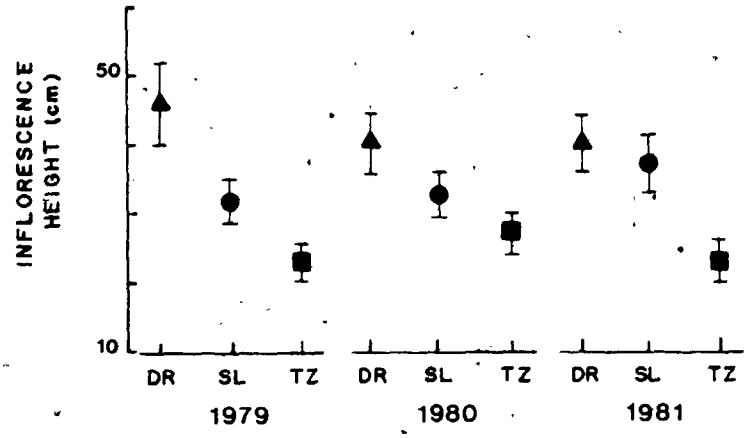
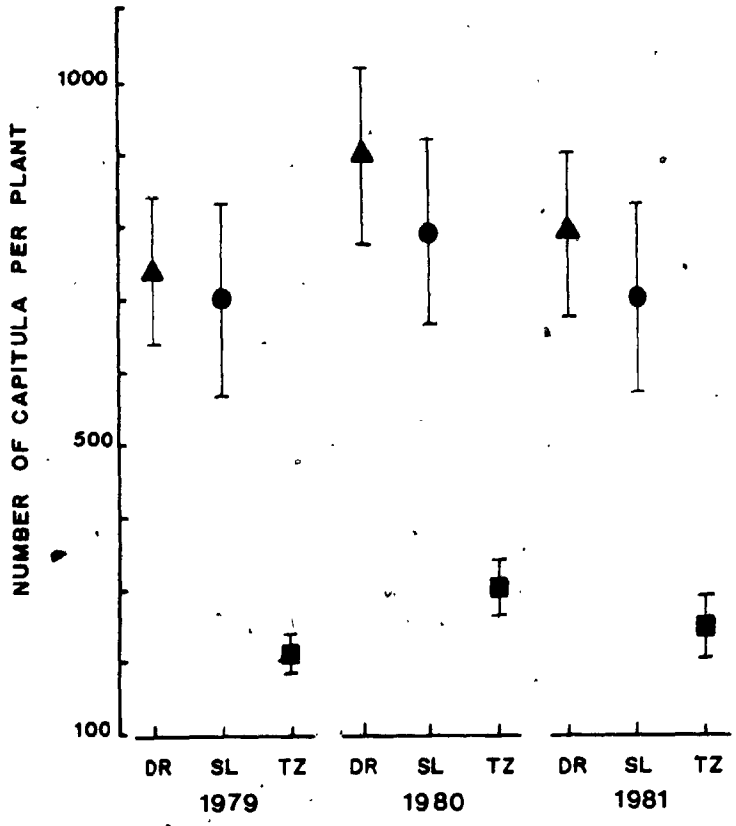
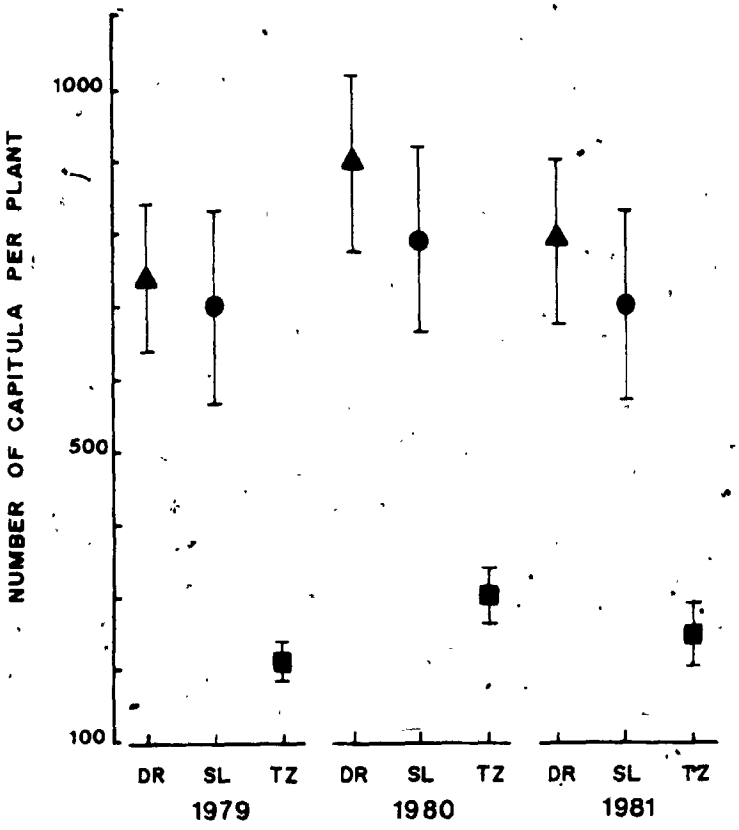

50
10
INFLORESCENCE HEIGHT (cm)
DR
SL
TZ
DR
SL
TZ
DR
SL
TZ
1979
1980
1981

Figure 6.6 Means and standard errors of number of capitula per plant in the dune ridge, slack and transition zone in each of three years.


NUMBER OF CAPITULA PER PLANT
1000
500
100
DR
SL
TZ
DR
SL
TZ
DR
SL
TZ
1979
1980
1981


NUMBER OF CAPITULA PER PLANT
1000
500
100
DR
SL
TZ
DR
SL
TZ
DR
SL
TZ
1979
1980
1981

| SOURCE | SS | DF | MS | F | SIGN. | b |
|---|---|---|---|---|---|---|
| HABITAT | 8.42 | 2 | 4.21 | 17.41 | *** | |
| YEAR | 0.47 | 2 | 0.23 | 0.97 | | |
| H x Y | 1.77 | 4 | 0.44 | 1.83 | | |
| HEIGHT | 66.18 | 1 | 66.18 | 273.62 | *** | 1.28 |
| DAMAGE | 0.30 | 1 | 0.30 | 1.26 | | 0.10 |
| ALL COV. | 66.31 | 2 | 33.15 | 137.07 | *** | |
| ERROR | 36.28 | 150 | 0.24 | | | |

Table 6.4 Analysis of covariance of number of capitula per plant among years and habitats, with inflorescence height and damage as covariates. H x Y is the interaction between habitat and year. Significance: *** $p<0.001$.

adjusted for the effect of inflorescence height are shown in Table 6.5. Means of dune ridge plants were consistently adjusted downwards, and transition zone means upwards, but even with adjustment, differences in means were still apparent between the dune ridge and slack on one hand, and transition zone on the other, as indicated in Figure 6.6. The added information on the effect of height indicates that dune ridge and slack plants were "bushier" (had more capitula per cm of inflorescence height) than transition zone plants.

6.3.2.4. Seeds per capitulum

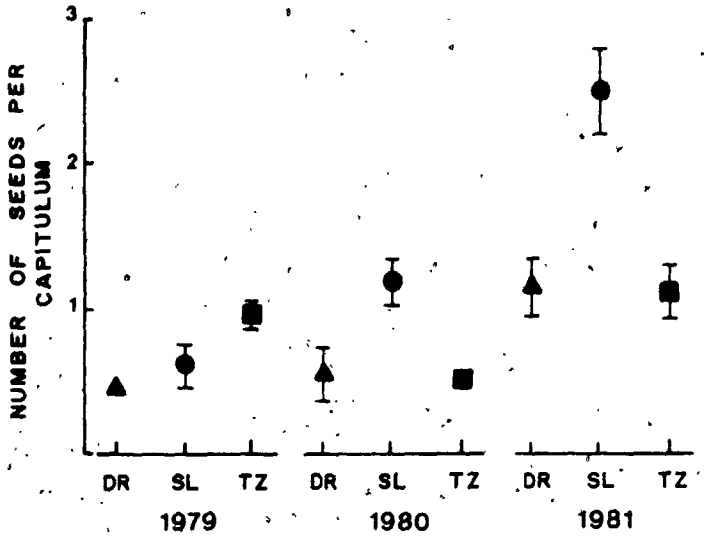
The number of seeds per capitulum is shown in Figure 6.7. The two-way analysis of variance of seeds per capitulum among habitats and years showed a significant interaction between the two grouping variables ($F_{4,161}$ = 4.66; p = 0.001). This was expected, as in 1979 transition zone plants had the highest mean seed production per capitulum but in both other years slack plants had the highest mean. Years and habitats were thus analysed separately by one-way analyses of variance. In 1979 there was a significant difference among habitat means ($F_{2,53}$ = 6.25; p<0.01). The comparison of means test showed significant differences at the 0.05 probability level between the transition zone and both other habitats. In 1980 the analysis of variance showed no significant differences among the means ($F_{2,38}$ = 2.98; p>0.05). In 1981, the analysis showed significant differences ($F_{2,72}$ = 7.95; p<0.001) between the slack and the other two habitats. Thus within two out of three years there were significant differences in mean seed production per capitulum between habitats, but which habitat produced plants with the

MEAN NUMBER ($LOG_e$) OF CAPITULA PER PLANT

| YEAR | HABITAT | $\bar{x} \pm$ S.E. | ADJ. $\bar{x}$ |
|---|---|---|---|
| 1979 | DUNE RIDGE | 6.35 ± 0.78 | 5.93 |
| | SLACK | 6.25 ± 0.88 | 6.25 |
| | TRANSITION ZONE | 4.99 ± 0.83 | 5.34 |
| 1980 | DUNE RIDGE | 6.49 ± 1.10 | 6.14 |
| | SLACK | 6.24 ± 0.87 | 5.93 |
| | TRANSITION ZONE | 5.40 ± 0.85 | 5.56 |
| 1981 | DUNE RIDGE | 6.50 ± 0.72 | 6.15 |
| | SLACK | 6.29 ± 0.83 | 6.05 |
| | TRANSITION ZONE | 5.18 ± 0.90 | 5.68 |

Table 6.5 Means and standard errors and adjusted means of $log_e$ capitulum number in three habitats during 1979, 1980 and 1981, derived from the analysis of covariance of $log_e$ capitulum number on inflorescence height and damage.

Figure 6.7 Means and standard errors of number of seeds per capitulum in the dune ridge, slack and transition zone in each of three years.


NUMBER OF SEEDS PER CAPITULUM
3
2
1
DR
SL
TZ
DR
SL
TZ
DR
SL
TZ
1979
1980
1981

highest seed number per capitulum was not consistent.

All habitats showed differences in mean seed production per capitulum among years ($F_{2,44} = 6.95$; $p<0.05$; $F_{2,47} = 12.42$; $p<0.001$; $F_{2,70} = 7.17$; $p<0.01$ in the dune ridge, slack and transition zone respectively). In the dune ridge, differences were found between 1981 and the other two years. In the slack only the difference in means between 1979 and 1980 was significant. In the transition zone the means test revealed differences between 1980 and the other two years.

The estimated percentage of reproductive potential actually fulfilled is presented in Table 6.6. The highest percentage of filled ovules occurred in 1981 in all three habitats. The lowest values in the dune ridge and slack occurred in 1979 and both these values were lower than that in the transition zone for the same year. Fertilization success was lowest in the transition zone in 1980.

Correlations between the square-root transformed seed production per capitulum and any of the four height variables (total height, average height, inflorescence height and average inflorescence height) were not significant except in the transition zone. The correlation between seed production per capitulum and average height was significant in this habitat in 1979 ($r_{19} = 0.68$; $p<0.01$). The correlation between seed production and total height was also significant at this time ($r_{19} = 0.43$; $p<0.05$).

| | PERCENT FILLED OVULES | | |
|---|---|---|---|
| HABITAT | 1979 | 1980 | 1981 |
| DUNE RIDGE | 4.0 | 8.2 | 15.8 |
| SLACK | 9.7 | 14.7 | 34.4 |
| TRANSITION ZONE | 13.2 | 6.5 | 15.8 |

Table 6.6 Percentage of filled ovules per 20 capitula based on an observed maximum of eight ovules per capitulum.

6.3.2.5. Effect of damage

Almost 90% of the plants examined in the slack showed some damage to the capitula, whereas 55% of dune ridge plants and 42% of transition zone plants were affected. The relationship between the total number of seeds (mature, immature and shrivelled) and damage in 20 capitula examined per plant in 1981 is presented in Table 6.7. The total number of seeds and the total number of damaged seeds were both highest in the slack. Sixteen percent of all capitula examined were affected in the slack, compared to approximately 5% in the dune ridge and 3% in the transition zone. The correlation between the number of seeds and number of damaged capitula was significant only in the slack, where a high degree of damage was associated with low seed number. This relationship is shown graphically in Figure 6.8, which presents the total number of seeds per 20 capitula and the number of capitula with visible insect damage. In the dune ridge and transition zone little relationship is evident with most values clumped at low values of both. In the slack, no effect was apparent in plants with up to 15% damaged capitula. The lack of relationship in the transition zone and dune ridge may reflect the fact that very few plants had more than 5% of the capitula damaged. A G test of independence between habitats and damage revealed highly significant differences ($\chi_4^2 = 29.21$; $p<0.001$).

Plants in the dune ridge had the greatest percentage of mature, fully formed seeds (Table 6.8). The percentage of both shrivelled and immature seeds was highest in the transation zone. Differences among habitats in the percentage of mature and shrivelled seeds were significant ($\chi^2_2 = 26.06$; $p<0.001$). The percentage of undeveloped seeds was low in all habitats (less

| HABITAT | DAMAGED CAP./20 CAP. | | SEEDS/20 CAP. | r |
|---|---|---|---|---|
| | $\bar{X} \pm$ S.E. | % | $\bar{X} \pm$ S.E. | |
| DUNE RIDGE | 1.07 ± 0.25 | 5.3 | 35.10 ± 3.69 | 0.10 |
| SLACK | 3.20 ± 0.52 | 16.0 | 53.69 ± 5.30 | -0.38* |
| TRANSITION ZONE | 0.61 ± 0.16 | 3.0 | 28.21 ± 3.24 | -0.20 |

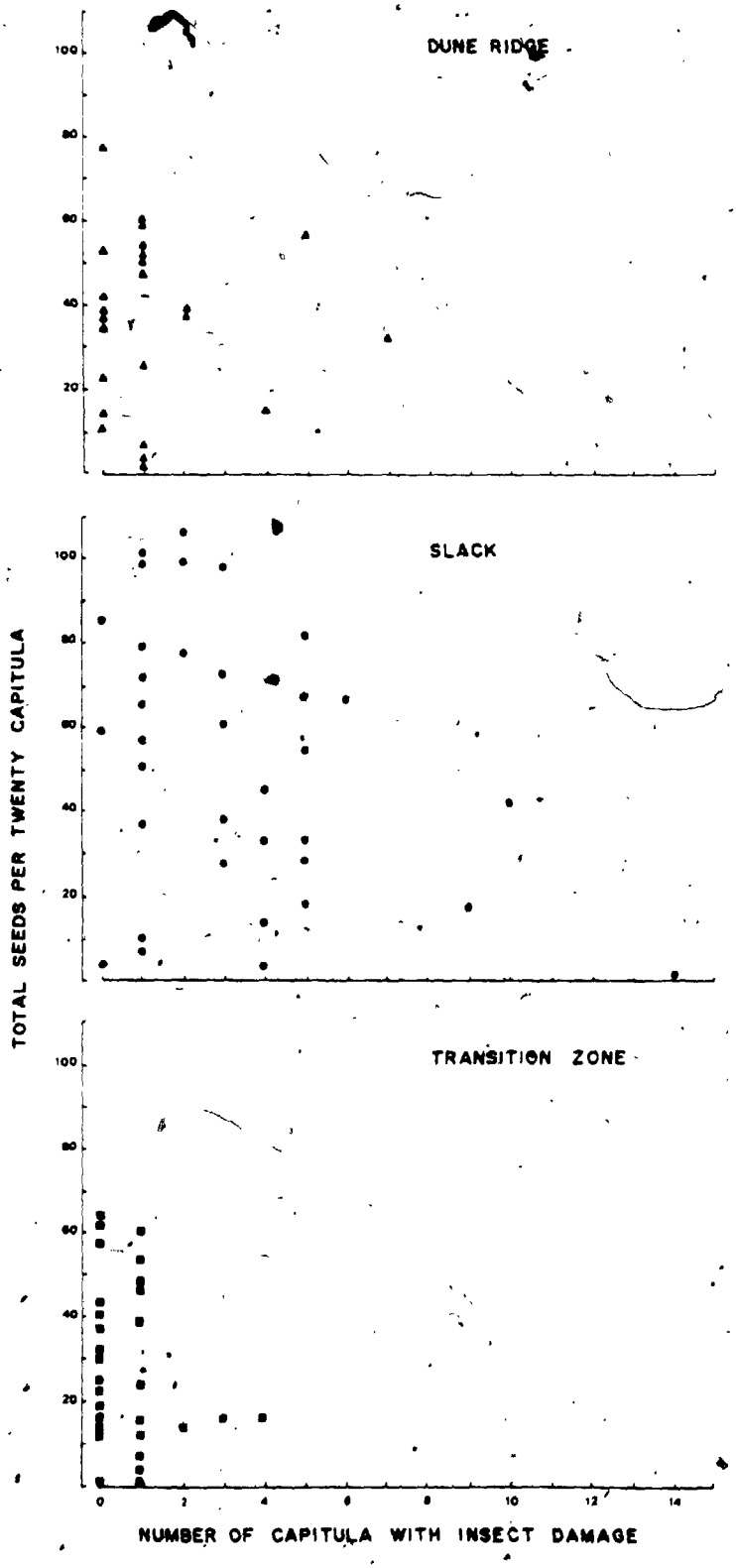
Table 6.7 Means ($\bar{X}$) and standard errors (S.E.) of capitula damaged, out of 20 examined per plant, and seeds per 20 capitula. The % damaged capitula per plant was estimated from the number of capitula damaged of 20 examined and the number of capitula per plant. The correlation (r) between number of seeds per 20 capitula and the number of damaged capitula is also presented for each habitat, with a significance level of $p<0.05$ denoted by *. Number of plants examined per habitat was 29, 35 and 33 for the dune ridge, slack and transition zone respectively.

CONDITION OF SEEDS

| HABITAT | MATURE | | SHRIVELLED | | UNDEVELOPED | | TOTAL |
|---|---|---|---|---|---|---|---|
| | n | % | n | % | n | % | n |
| DUNE RIDGE | 865 | 85.0 | 149 | 14.6 | 3 | 0.3 | 1017 |
| SLACK | 1486 | 79.1 | 389 | 20.7 | 4 | 0.2 | 1879 |
| TRANS-ITION ZONE | 683 | 73.4 | 238 | 25.6 | 9 | 1.0 | 930 |

Table 6.8 The total number of seeds counted in 20 capitula per plant, and the number and percentage of mature, shrivelled and undeveloped seeds from three habitats in 1981. The number of plants examined in each habitat was 29, 35 and 33 from the dune ridge, slack and transition zone respectively.

Figure 6.8 Relationship between total number of seeds in 20 capitula per plant and the number of capitula visibly damaged by insects of those 20 capitula in the dune ridge, slack and transition zone in 1981.


DUNE RIDGE
SLACK
TRANSITION ZONE
TOTAL SEEDS PER TWENTY CAPITULA
NUMBER OF CAPITULA WITH INSECT DAMAGE
100
80
60
40
20
0
2
4
6
8
10
12
14

than 1.0%). In the dune ridge large numbers of deformed seeds tended to occur with large numbers of mature seeds, though most plants had a few shrivelled seeds (Figure 6.9). The majority of plants in the slack also had a small number of deformed seeds regardless of the number of mature seeds. Some plants with large numbers of seeds had a large number of shrivelled seeds, and two plants had a many more shrivelled seeds than fully formed ones. This pattern was repeated in transition zone plants.

6.3.2.6. Harvest date

The relationship between harvest date and seed production in 1991 is shown in Figure 6.10. Although confidence limits among habitats were very different, despite the $\log_e$ transformation, it is clear that means in the dune ridge and slack varied little among harvest dates. Transition zone plants not only matured later than plants in other habitats but showed a clear difference in means among dates. Plants harvested earliest produced the largest number of seeds, and there was a decrease in seed production with each successive harvest date.

6.3.2.7. Fall rosette diameter

There was no relationship between fall rosette diameter and height or capitulum number the following year, except in the dune ridge where variations in the previous fall's rosette diameter accounted for 75% of the variation in inflorescence height the following year, and 73% of the variation in capitulum number.

Figure 5.2 The relationship between the number of mature seeds in 20 capitula per plant and the number of shrivelled seeds in the same 20 capitula, in three habitats in 1981.

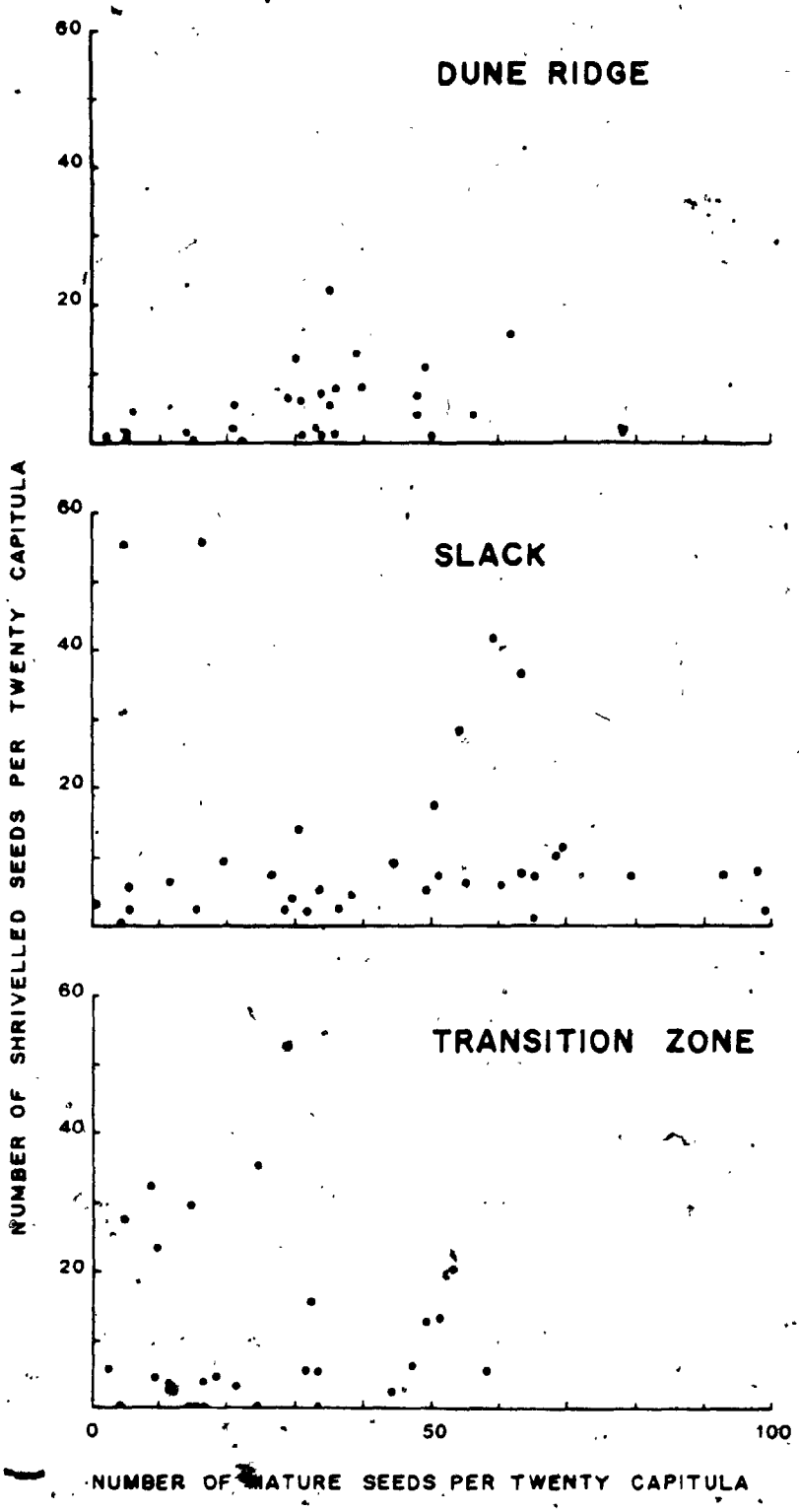
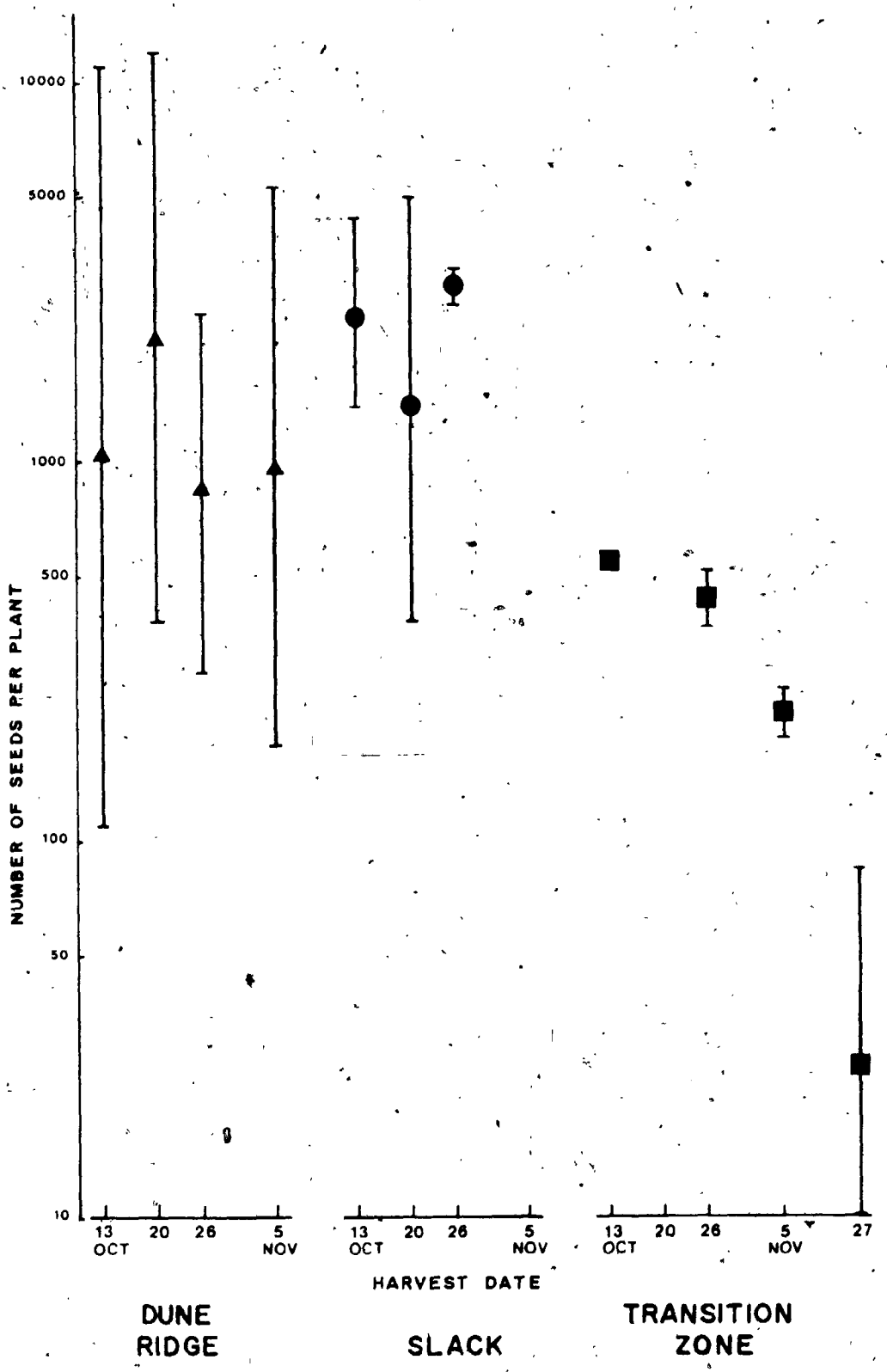

DUNE RIDGE
SLACK
TRANSITION ZONE
60
40
20
0
50
100
NUMBER OF SHRIVELLED SEEDS PER TWENTY CAPITULA
NUMBER OF MATURE SEEDS PER TWENTY CAPITULA

Figure 6.10 Arithmetic means and 95% confidence limits (from $\log_e$ transformed data) of seed number per plant at five harvest dates in 1981 in the dune ridge, slack and transition zone.


10000
5000
1000
500
100
50
10
NUMBER OF SEEDS PER PLANT
13 OCT
20
26
5 NOV
13 OCT
20
26
5 NOV
13 OCT
20
26
5 NOV
27
HARVEST DATE
DUNE RIDGE
SLACK
TRANSITION ZONE

6.3.3. Seed rain

Means and standard errors of the density of reproductive plants, the geometric means of seed number per plant, and their product (estimated seed rain) for each habitat in 1980 and 1981 are shown in Table 6.9. Estimated seed rain was remarkably constant in the dune ridge over the two years studied. It varied by a factor of four in the transition zone, mainly due to a difference in the number of reproductive plants. Seed rain was six times as high in 1981 as in 1980 in the slack, due to increases in both seed number and density of flowering plants.

6.3.4. Seed mass

Mean seed mass ± 1 standard error was $3.03 \times 10^{-3}$mg ± 0.22 in the dune ridge, 2.61 ± 0.21 in the slack and 2.49 ± 0.19 in the transition zone in 1980. The analysis of variance showed significant differences among habitats ($F_{2,71} = 3.202$; $p<0.05$). The Tukey-Kramer test showed significant differences only between the dune ridge and transition zone.

Correlations between seed number and seed mass were not significant at the 0.05 level in any habitat, but a negative correlation between $\log_e$ seed number and seed mass in the slack was significant at the 0.10 level.

6.3.5. Fate of individuals

6.3.5.1. In the field

The number and percent of plants attempting flowering that died

| YEAR | HABITAT | DENSITY $m^{-2}$ $\bar{X}_R \pm$ S.E. | SEEDS PER PLANT $\bar{Y}_G$ | SEED RAIN $m^{-2}$ $\bar{X}_R \times \bar{Y}_G$ |
|---|---|---|---|---|
| 1980 | DUNE RIDGE | 0.17 ± 0.07 | 41[illegible] | [illegible]1 |
| | SLACK | 0.21 ± 0.09 | 633 | 133 |
| | TRANSITION ZONE | 0.23 ± 0.09 | 107 | 25 |
| 1981 | DUNE RIDGE | 0.41 ± 0.19 | 181 | 74 |
| | SLACK | 0.79 ± 0.21 | 1075 | 850 |
| | TRANSITION ZONE | 0.67 ± 0.15 | 140 | 94 |

Table 6.9 Estimated seed rain per square metre in the dune ridge, slack and transition zone in 1980 and 1981, based on the density of reproductive plants $\bar{X}_R$ and the geometric mean of seed production $\bar{Y}_G$.

during flowering, suffered loss of the floral meristem, or flowered successfully within each habitat during each year are presented in Table 6.10. Though year to year variability existed major trends appeared consistent. Overall mortality during flowering was lowest in the dune ridge and highest in the slack. In the transition zone, mortality was intermediate between the dune ridge and slack with a narrower range between years.

Death of just the floral meristem was highest in the transition zone, though rates were low (less than 10% in all years) even in this habitat. Of plants which lost the floral meristem during their initial flowering attempt, none attempted flowering again in the slack (Table 6.11). Approximately half flowered again in the dune ridge, and 25% in the transition zone.

Overall flowering success was highest in the dune ridge and similar between the transition zone and slack. This was statistically significant according to a G test of flowering success among habitats ($\chi^2_2 = 18.10$; $p<0.001$). In the dune ridge, the lowest success rate occurred in 1979, due to the high mortality that year. In the transition zone, flowering was least successful in 1980, because of combined high mortality and floral meristem loss.

The fate of plants that flowered successfully in a given year is presented in Table 6.12. Data are not presented for plants which flowered in 1981, as no attempt was made to follow their fate in 1982. In the slack, all plants that flowered successfully died before the following season. Postflowering survival was low in the dune ridge, and none of the survivors

| | | DIED DURING FLOWERING | | LOST FL. MERISTEM | | FLOWERED SUCCESSFULLY | |
|---|---|---|---|---|---|---|---|
| HABITAT | YEAR | n | % | n | % | n | % |
| DUNE RIDGE | 1978 | 8 | 5 | 4 | 2 | 148 | 93 |
| | 1979 | 14 | 25 | 2 | 4 | 39 | 71 |
| | 1980 | 0 | 0 | 1 | 8 | 12 | 92 |
| | 1981 | 1 | 6 | 0 | 0 | 15 | 94 |
| | TOTAL | 23 | 9 | 7 | 2 | 215 | 88 |
| SLACK | 1978 | 30 | 27 | 2 | 2 | 79 | 71 |
| | 1979 | 9 | 32 | 0 | 0 | 19 | 68 |
| | 1980 | 0 | 0 | 0 | 0 | 12 | 100 |
| | 1981 | 5 | 20 | 1 | 4 | 19 | 76 |
| | TOTAL | 44 | 25 | 3 | 2 | 130 | 73 |
| TRANS-ITION ZONE | 1978 | 13 | 19 | 6 | 9 | 49 | 70 |
| | 1979 | 7 | 20 | 2 | 6 | 25 | 74 |
| | 1980 | 6 | 27 | 2 | 9 | 14 | 64 |
| | 1981 | 2 | 7 | 1 | 4 | 25 | 93 |
| | TOTAL | 28 | 18 | 11 | 7 | 113 | 74 |

Table 6.10 The outcome (in numbers and percentages of plants) of flowering attempts in 1978-81 in the dune ridge, slack and transition zone. Possible fates were: death prior to successful flowering, loss of floral meristem before successful flowering and successful completion of all flowering stages.

| HABITAT | YEAR | DIED VEGETATIVE | FLOWERED AGAIN | TOTAL |
|---|---|---|---|---|
| DUNE RIDGE | 1978 | 1 | 3 | 4 |
| | 1979 | 2 | 3 | 5 |
| | 1980 | 1 | 0 | 1 |
| | 1981 | | | 0 |
| | TOTAL | 4 | 3 | |
| SLACK | 1978 | 2 | 0 | 2 |
| | 1979 | 0 | 0 | 0 |
| | 1980 | 0 | 0 | 0 |
| | 1981 | 1 | | 1 |
| | TOTAL | 3 | 0 | 3 |
| TRANSITION ZONE | 1978 | 5 | 1 | 6 |
| | 1979 | 2 | 0 | 2 |
| | 1980 | 1 | 1 | 2 |
| | 1981 | | | 1 |
| | TOTAL | 8 | 2 | 11 |

Table 6.11 The fate of flowering plants after losing the floral meristem before successful flowering, reported for 1978-1981 in the dune ridge, slack and transition zone. Possible fates were flowering again or dying in the following year/years.

| HABITAT | YEAR | n | DIED | VEG. | FL. | SURV. |
|---|---|---|---|---|---|---|
| | | | % | % | % | % |
| DUNE RIDGE | 1978 | 149 | 96.6 | 3.4 | 0.0 | 3.4 |
| | 1979 | 39 | 94.9 | 9.5 | 0.0 | 9.5 |
| | 1980 | 12 | 100.0 | 0.0 | 0.0 | 0.0 |
| | TOTAL | 200 | 97.0 | 3.5 | 0.0 | 3.5 |
| SLACK | 1978 | 79 | 100.0 | 0.0 | 0.0 | 0.0 |
| | 1979 | 19 | 100.0 | 0.0 | 0.0 | 0.0 |
| | 1980 | 13 | 100.0 | 0.0 | 0.0 | 0.0 |
| | TOTAL | 111 | 100.0 | 0.0 | 0.0 | 0.0 |
| TRANS-ITION ZONE | 1978 | 49 | 83.7 | 10.2 | 14.7 | 16.3 |
| | 1979 | 25 | 96.0 | 0.0 | 4.0 | 4.0 |
| | 1980 | 14 | 92.9 | 7.0 | 0.0 | 7.0 |
| | TOTAL | 88 | 88.6 | 6.8 | 4.5 | 11.4 |

Table 6.12 The fate of plants that flowered successfully during a given year. the percentage that died before the following growing season (DIED), that lived during at least part of the following season in a reverted juvenile (post-flowering vegetative) phase (VEG.); and that flowered again (FL.) in a subsequent season. Total post-flowering survival (SURV.) is also given.

flowered again. They survived in a postflowering vegetative state for up to a few months before dying. Postflowering survival was higher in the transition zone with much year to year variability, ranging from 4% in 1979 to 16% in 1978. Differences in post-flowering survival among habitats (pooled over years) were statistically significant ($\chi^2_2 = 14.19$; $p<0.01$).

A small number of plants (4.5%) flowered again in the transition zone, with a wide range between years (Table 6.12). Fifteen percent of the plants flowering in 1978 flowered again. None of the plants flowering in 1980 flowered again. However, 7% of the plants which flowered during that year survived, and may have flowered in 1982 or later. One plant flowered three times. The existence of polycarpy in the field appeared to be confined to the transition zone. However, if postflowering vegetative survival may be taken as an indication of potential for polycarpy, that potential is also present in dune ridge plants.

6.3.5.2. In common garden conditions

At Labatt Field Station, all of the surviving plants flowered synchronously in 1981, with a schedule closely following that in the dune ridge. None survived the following winter.

Initiation of flowering in the greenhouse at U.W.O. was continuous throughout the study period. Flowering patterns in the greenhouse are presented in more detail in Table 6.13. Three basic patterns were observed. (1) A few plants showed one distinct flowering event, with the initiation of one or more floral meristems at the same time. The flowering event ended

## GREENHOUSE EXPERIMENTS

| FATE | HB | DR | SL | TZ | TOTAL |
|---|---|---|---|---|---|
| Died before attempting flowering | 4 | 3 | 3 | 1 | 11 |
| Attempted flowering; died before completion | 1 | 1 | 0 | 0 | 2 |
| Flowered once; died following, or during postflowering vegetative phase | 2 | 0 | 2 | 0 | 4 |
| Flowered at least twice, with vegetative phase dividing flowering events | 2 | 2 | 4 | 1 | 9 |
| Flowered continuously for at least a year before termination of the study | 2 | 4 | 3 | 3 | 12 |
| Flowered 1982; alive at termination of the study | 2 | 0 | 2 | 1 | 5 |
| Remained juvenile until termination of the study | 3 | 3 | 1 | 7 | 14 |
| Total sample | 15 | 13 | 15 | 13 | 56 |

Table 6.13 The number of plants in each fate category, of plants which were cloned from mother plants from the high beach (HB), dune ridge (DR), slack (SL), and transition zone (TZ) and grown in the greenhouse from June 1980 to December 1982.

with the death of the inflorescence and a return to the vegetative state followed by death, or death to the entire plant immediately following flowering. (2) Some plants from all habitats had two or more distinct flowering events, separated by a postflowering vegetative phase. (3) The most common pattern in flowering plants was continuous flowering; as one inflorescence aged, new ones were initiated. Again this pattern occurred in plants from all habitats.

6.3.6. Postflowering survival and height during flowering

The means and standard errors of total height of plants classified by postflowering fate is presented in Table 6.14. Though plants in the dune ridge which survived appeared much smaller than those that didn't, the difference was not significant ($t_{72} = 1.29$; $p>0.05$). In the transition zone plants which died immediately following flowering appeared larger than those which survived vegetatively or flowered again, but the difference was only significant between nonsurvivors and polycarpic plants in their first flowering season.

6.4 Discussion

Plants in the transition zone at Pinery flower approximately a week later than plants in the dune ridge and slack. In populations of *Anthyllis vulneraria* growing on a coastal sand system Sterk (1975) found that inland populations flowered a month earlier than coastal ones did, but no data were available on genetic control. Year to year variation within habitats at Pinery indicate that environmental factors in part control flowering

| HABITAT | POSTFLOWERING FATE | n | TOTAL HEIGHT $\bar{X}$ (cm) ± S.E. |
|---|---|---|---|
| DUNE RIDGE | Died | 67 | 74.60 ± 5.17 |
| | Lived vegetatively | 7 | 52.71 ± 17.97 |
| TRANSITION ZONE | Died | 72 | 45.93 ± 2.63a |
| | Lived vegetatively | 6 | 28.86 ± 4.05 |
| | Flowered again | 4 | 28.50 ± 2.40a |
| | Height at second flowering | 4 | 34.30 ± 17.19 |

Table 6.14 Means ($\bar{X}$) and standard errors (S.E.) of total height of flowering plants, classified according to habitat and fate after the first flowering event. No plants from the slack habitat are included since none survived after the first flowering. Means followed by the letter 'a' are significantly different at the 5% probability level.

date within populations. Since plants at Labatt Field Station flowered synchronously regardless of habitat of origin, and greenhouse plants flowered continuously, it can be assumed that flowering date differences at Pinery are not genetically determined. The slower growth rate of transition zone plants (Chapter 5) may contribute to their later flowering.

Plants grown at Labatt Field Station under noncompetitive conditions flowered with a schedule closely approximating that in the dune ridge. Palmblad (1968) found that populations of *Senecio viscosus* flowered earlier under low densities than under high densities, but timing of anthesis in *S. sylvaticus* was independent of density. Other environmental differences aside from the absence of near neighbours existed between Pinery habitats and the field station, notably in soil fertility and soil texture. McNeilly and Antonovics (1967) found that populations of *Agrostis tenuis* and *Anthoxanthum odoratum* growing in warmer, drier soils flowered earlier and this difference was replicable in a uniform garden. The soil at Labatt Field Station is a well-developed clay loam, with a high organic matter content. Although no fertilizer was added to the soil at Labatt's during the study, the field had been fertilized in previous years and some residue might be expected to remain.

The effect of temporal differences in flowering in terms of gene flow between populations depends on the spatial proximity of those populations (Faegri and van der Pijl 1979) and on their relative active flowering periods (Whitehead 1969). Although most pollen is dispersed within a very small radius of the mother plant (Levin and Kerster 1974; Friedman and Orshan 1975) the possibility of gene flow based on spatial proximity still remains at larger

larger distances, especially if the populations are linked by at least some intermediately placed plants. Given the protandry of *A. campestris*, the timing differences among the habitats, and the short viability period of Anthemidae pollen (Heywood and Humphries 1977), it is unlikely that dune ridge plants are ever directly pollinated by transition zone plants, or vice versa. However, the flowering schedule of slack plants overlaps that of both dune ridge and transition zone plants, thus providing intermediates. The prevailing winds are onshore at this time of year and would blow pollen from the dune ridge and slack towards the transition zone (Pinery Meteorological Station data), but the pollen cloud would be densest well before plants in the transition zone were stigmatically receptive. Though gene flow between populations in the three habitats studied may be small it cannot be dismissed entirely. Antonovics (1968) states that gene flow among populations must be considered the rule rather than the exception.

A more direct effect of the delayed flowering schedule in the transition zone may be the effect on seed production. Seed set was reduced in both early and late flowering individuals of *Claytonia virginica* (Schemske 1977) and *Hybanthus prunifolia* (Augspurger 1981). Pollen availability was the limiting factor in both these cases due to pollinator scarcity. Pollen availability may be a factor in reduced seed set in *A. campestris* populations as well, particularly in the transition zone. Many flowers in the transition zone remained stigmatically receptive long after the period of pollen dispersal, and plants which were harvested latest in the transition zone produced the fewest seeds. This suggests that late flowering plants were not as fully fertilized as plants which flowered earlier. A tradeoff between

early and late flowering may be occurring. Delayed flowering may allow more time for resource accumulation and consequent higher fecundity, but delaying too long may reduce the probability of fertilization.

The actualization of reproductive potential (the number of ovules actually fertilized) is also under more stochastic influences. Pollination conditions (wind velocity and direction, precipitation) will vary from year to year, and also within a year, but not on a predictable basis. Conditions affecting the dynamics of the insect populations which may reduce seed production can also be expected to vary between and within years.

Flowering schedules affect the conditions under which seeds mature, which in turn affect seed characteristics. Alexander and Wulff (1985) found that high temperatures decreased seed weight in *Plantago lanceolata* and that small seeds had a higher germination rate. Stearns (1960) obtained similar results in *P. aristata*. Smaller seeds in this species produced more vigorous seedlings. *Rumex crispus* seeds harvested before full maturation produced smaller seeds and seedlings but this initial effect was of short duration (Maun 1974). Differences in seed mass in *A. campestris* observed at Pinery may be in part a result of environmental conditions during maturation, but they may also result from smaller maternal investment by less vigorous mother plants. The effect of low seed weight on germination and growth in *A. campestris* is unknown, but the results reported above for other species preclude assuming that seeds from the transition zone are less fit than those from the other habitats.

Both the slack and the transition zone habitats appear to be less predictable than the dune ridge in the factors affecting future reproductive output. Fall rosette diameter, though useful in predicting the probability of flowering the following season (Chapter 5), was useful as a predictor of fecundity only in the dune ridge. Both biotic (herbivores, increased competition on a microenvironmental level) and abiotic factors (disturbance, water stress, freezing) may be operative in the eight month interval (September-June) between rosette diameter measurement and bolting. Other studies have used early season rosette diameter as a predictor of fecundity during the same season with more reliable results.

Plants growing in the transition zone were not only shorter but also less bushy than those in the other two habitats. Since all plants grown at Labatt Field Station were large and bushy, regardless of their habitat of origin, three-dimensional size is likely to be primarily environmentally controlled, again by factors of competition and soil fertility. Thus there may not be a genetic difference in reproductive potential, measured by the number of capitula, but there is certainly a phenotypic difference influenced by habitat.

Damage to the mother plant was not a factor in seed production in *A. campestris*. Hartnett and Abrahamson (1979) found that three species of gall insects infesting populations of *Solidago canadensis* differed in the quantity and quality of damage inflicted, though all showed reduced seed reproductive allocation. Both the ball gall and elliptical gall affected propagule weight, a factor not investigated here.

Insect damage within the capitulum affected seed production only in the slack. Capitula infestation affected twice as many plants in the slack as in the dune ridge and transition zone, and three to five times as many capitula. Seed production was unaffected in all habitats in plants with low levels of capitulum infestation. In the slack, plants with more than 15% of the capitula damaged showed reduced seed production. Plants in other habitats did not sustain this degree of damage.

The presence of shrivelled seeds could indicate presence of a pathogen. Alternatively, it may mean that seeds undergo competition for resources from the mother plant, and that a proportion of fertilized seeds are aborted if resources are limited. The presence of a large number of deformed seeds with a large number of fully developed seeds would support the latter hypothesis. The presence of large numbers of shrivelled seeds with few fully formed seeds supports a pathogen hypothesis. If these hypotheses are true, it is probable that both factors are at work in the transition zone and slack, but the dune ridge appears to be comparatively free of pathogens.

Despite the fact that seed production differed among habitats, the pattern of seed production by individuals within habitats was similar. Most of the seeds produced in a population are produced by only a small proportion of the population. This concurs with results from populations of *Phlox drummondii* (Leverich and Levin 1979) and *Lupinus texensis* (Schaal 1980).

Flowering success, the successful completion of all stages from bolting to seed maturation, was highest in the dune ridge, with little difference

between the slack and transition zone. Flowering success has two components in populations of *A. campestris*, survival and maintenance of the floral meristem. In the transition zone and dune ridge, destruction of the floral meristem may simply postpone flowering, as it does in *Senecio jacobaea* (Cameron 1935). In the slack, once a plant's floral meristem has died, the plant is reproductively dead. Mortality pressures appear to be stronger in the slack at all life stages (Chapters 4 and 5) including the reproductive phase. These stresses probably inhibit recovery of a damaged plant in the slack more so than in the other two habitats.

Senescence in monocarps has been linked to the release of a senescence hormone by the maturing seeds or other reproductive structures (Woolhouse 1983). If seed or capitulum production is low, an insufficient amount of senescence hormone may be released to promote death. An evolutionary interpretation of this apparent "suicide" would suggest that the senescence hormone triggers the translocation of available resources to the developing seeds. Plants with few seeds would thus retain enough (untranslocated) resources to survive flowering and have a "second chance" at reproduction. Observations from this study support this hypothesis. In the slack, large numbers of seeds combine with large numbers of capitula, and no postflowering survival is observed. In the dune ridge, capitulum number is high but seed number is much less than in the slack, and some postflowering survival is observed. In the transition zone, where both seed number and capitulum number are low, and in the greenhouse, where no seed production was observed, the lack of sufficient senescence hormone may allow postflowering survival and a second flowering season.

Although polycarpy only occurs in the transition zone, the potential for polycarpy appears latent in plants from other habitats. A post-flowering vegetative period is sometimes observed on the dune ridge, although death always preceded a second flowering season in this study. In the greenhouse, plants from all habitats were observed to flower continuously or repeatedly. Repeated flowering provides direct evidence of potential polycarpy. Continuous flowering is more problematic, since it raises the question of definitions of "monocarpy" and "polycarpy". These plants can be considered monocarpic since there is a single interval during which flowering never ceases, a single reproductive event. They may also be considered polycarpic because not all reproductive units are initiated at the same time. In natural environments, seasonality cues probably prevent initiation from occurring in this way. The maintenance of the potential for polycarpy within these phenotypically monocarpic populations may simply be a result of the indeterminate nature of their growth pattern.

## 6.5 Summary

1. Plants in the dune ridge and slack started flowering at the same time, about a week earlier than in the transition zone. In the dune ridge, pollen release and fertilization occurred rapidly. In the slack, both occurred over a longer period of time, but not as prolonged as in the transition zone. In this latter habitat many plants remained receptive well beyond the period of active pollen release in all habitats.

2. Slack plants had the highest fecundity, and transition zone plants the lowest in all three

years. Seed production per capitulum varied among habitats and years. Insect damage to seeds was directly related to total seed number in slack plants. Most of the seeds in each population were produced by only a few plants.

3. Seeds were heaviest in the dune ridge and lightest in the transition zone.

4. Flowering success was 88, 73 and 74% in the dune ridge, slack and transition zone respectively over all three years. Approximately 3.5% of flowering plants studied in the dune ridge survived the first flowering but none flowered again. No plants in the slack survived after flowering. In the transition zone, 11.4% survived flowering, and 4.5% flowered again.

5. Plants that flowered twice were smaller (total height) during their first flowering season than plants that died after the first flowering.

# CHAPTER 7

# DISCUSSION

The genetic component of a population's life history has been called its "strategy" whereas the phenotypic realization of the genetic potential has been referred to as its "tactics" (Harper and Ogden 1970). The results from the uniform garden experiments in this study suggest no (genetic) differentiation in strategy among the populations studied (Chapters 5 and 6). This chapter will discuss the population consequences of the habitat-related differences in life history parameters and suggest a model for the maintenance of facultative polycarpy within the populations studied.

The previous chapters have reported several aspects of the recruitment, survival, growth and reproduction of *Artemisia campestris* in the seedling (Chapter 4), juvenile (Chapter 5) and reproductive (Chapter 6) phases. The results of these chapters relevant to a discussion of life history tactics in *A. campestris* are summarized in Table 7A.

Baldwin (1982) found a clear separation in physical parameters between the dune ridge and slack ("open" habitats) and the transition zone ("closed"). This duality is not evident from an examinination of the life history characters of *Artemisia campestris* in these habitats. There is also no gradient of life history characters parallelling the successional

| VARIABLE | DUNE RIDGE | SLACK | TRANSITION ZONE |
|---|---|---|---|
| Emergence | lower | high* | lower |
| Survival | higher | low | higher |
| Rosette diameter | large | intermediate | small |
| Juvenile phase | short | intermediate | longer* |
| Flowering success | high | lower | lower |
| Flowering seasons | 1 | 1 | 1-3 |
| Post-flowering survival | low | 0 | higher* |
| Seeds produced | intermediate | many | few |
| Seed weight | heavier | intermediate | lighter |

Table 7.1 Comparative summary of life history variables in *Artemisia campestris* populations, reported in Chapters 4, 5 and 6 for the dune ridge, slack and transition zone. * denotes a large variance associated with the mean.

chronosequence in the three habitats, supporting the view presented in Chapter 1 that attempting to embed the results of this study in a successional model was inappropriate. Some of the life history characters appear to group two of the habitats together in opposition to the third, but the pair does not always have the same identity. Other variables allowed the habitats to be ranked rather than grouped, but again the ranks assigned to each habitat vary among characters.

The dune ridge and transition zone are similar in the emergence patterns observed. Emergence in both habitats was lower and less variable than in the slack. Two factors influence emergence, seed availability and safe site availability. Variance in seed availability (seed rain) may contribute to the high year to year variablity in emergence in the slack, but seed rain in the transition zone was also variable, though not as much as in the slack. The slack, being less protected by ground cover from the effects of the environment, probably has fewer safe sites than the other habitats in terms of moisture requirements for germination and emergence. The ground cover in the transition zone, while trapping moisture, also limits the space available for emergence. Thus the common pattern of low emergence and low variability in emergence seen in the dune ridge and transition zone may be caused by different factors: low variability in seed source in the dune ridge, and space limitation in the transition zone.

Seedling and juvenile survivorship were also similar in the dune ridge and transition zone, and higher at both stages than in the slack. Desiccation is the most probable primary mortality factor in all three habitats, and again the slack is less buffered against drought than the other two habitats

because of the sparse vegetation. But the effects of the environment are moderated in the dune ridge and transition zone in different ways, the transition zone through a dense forb ground cover, and the dune ridge through shrubby vegetation and its proximity to the lake, and hence to moist onshore breezes.

The impact of visible damage to juvenile plants is similar in the slack and transition zone. Plants in both habitats sustained more damage than those in the dune ridge. The presence of pathogens affecting seed production also seem to be confined to the slack and transition zone. Thus biotic factors affect the slack and the transition zone more extensively than the dune ridge. However, low seed production was only associated with insect damage in the slack, suggesting plants here are more heavily stressed by at least one biotic factor than the transition zone.

Among the ranked variables, plants in the dune ridge had the largest rosette diameter, and their growth rate over a year was also highest. They also had the largest rosette diameter "required" to flower, and more of them flowered at Age 3. In addition, they produced the tallest flowering plants, with the highest number of capitula, and the largest seeds. In all these variables, slack plants were intermediately ranked, and transition zone plants ranked lowest. Thus growth conditions appear to be the most favourable in the dune ridge. In the transition zone, reduction in growth early in the season suggests interference from other plants. In the slack, moisture stress may be limiting.

Despite the relatively high levels of biotic and abiotic stress apparent in slack populations, seed number was highest here, followed by the dune ridge and transition zone. It is possible that the same factor which prevents desiccation in the dune ridge, the onshore breeze, disperses the pollen cloud quickly from the habitat. The linear nature of the habitat, as well as its proximity to the lake, may reduce the number of pollen-laden plants that are upwind from a receptive one. Thus low fecundity may be a result of low pollen availability. Flowering schedules within the transition zone also suggest low pollen availability as an explanation for reduced fecundity in this habitat, though again lack of fertilization success was caused by different factors than in the dune ridge: delayed and prolonged flowering. In the slack, plants have the advantage of close proximity to other simultaneously flowering plants, in an area with enough shelter that the pollen clouds do not immediately disperse.

The pattern of these variables permits a characterization of the habitats as they affect the plants. The dune ridge appears to be the most constant habitat, with low and relatively unvarying levels of both biotic and abiotic factors, producing favourable growth conditions. The value of rosette diameter in predicting size during flowering in the following season was only high in this habitat, supporting this characterization. Plants in the transition zone appear to be affected primarily by biotic factors: density of co-occurring vegetation and herbivores. The slack is affected by biotic and abiotic factors, both stochastic and deterministic, making it the harshest and least predictable habitat. It is also the habitat in which the highest fecundity may be attained, and this may be what allows the

population to regenerate.

Life tables provide a convenient summary of life history variables, and also a method of examining their population consequences (Deevey 1947). Life tables for the three habitats are presented in Table 7.2. They are constructed from age specific survivorship $l_x$ and fecundity $b_x$, and also include estimates of the population replacement rates $R_0 = \Sigma l_x b_x$. Age-specific fecundities were calculated as the product of the probability of flowering at each age, the probability of successful flowering, the geometric mean of seed number pooled over years and emergence rate. Emergence rates were estimated by dividing emergence in 1981 by seed rain in 1980, and thus assumes no seed pool. Values obtained were 2.5%, 13.4% and 9.6% in the dune ridge, slack and transition zone respectively. Full calculations for age-specific fecundity are contained in Appendix IV.

Because the data are pooled over years, the life tables do not represent any single cohort, but do incorporate some of the observed year to year variability. Emergence rate is the only parameter for which only one year's data was available.

In the dune ridge, the population replacement rate was close to 1, as expected in a stable population. The replacement rate in the slack was 2.42, due entirely to high fecundity. The transition zone population also appears to be increasing dramatically, due to high survivorship and early maturity.

Emergence in 1981 was very high in the slack compared to 1980. If the emergence rate falls in some years to that seen in the dune ridge, 2.5%, the replacement rate would be 0.45. A cycle of "good" and "bad" years would

| HABITAT | AGE | $l_x$ | $b_x$ | $l_x b_x$ |
|---|---|---|---|---|
| DUNE RIDGE | 1 | 0.49 | | |
| | 2 | 0.39 | | |
| | 3 | 0.30 | 3.43 | 1.03 |
| | 4 | 0.07 | 2.11 | 0.15 |
| | 5 | 0.01 | 1.74 | 0.02 |
| $R_0$ | | | | 1.19 |
| SLACK | 1 | 0.27 | | |
| | 2 | 0.16 | | |
| | 3 | 0.07 | 23.48 | 1.64 |
| | 4 | 0.02 | 26.41 | 0.53 |
| | 5 | 0.01 | 24.46 | 0.25 |
| $R_0$ | | | | 2.42 |
| TRANSITION ZONE | 1 | 0.48 | | |
| | 2 | 0.48 | 1.19 | 0.57 |
| | 3 | 0.31 | 3.24 | 1.00 |
| | 4 | 0.12 | 2.90 | 0.35 |
| | 5 | 0.03 | 2.98 | 0.09 |
| $R_0$ | | | | 2.01 |

Table 7.2 Generalized life table for *Artemisia campestris* in the dune ridge, slack and transition zone. Data for the five age classes were pooled over 1979, 1980 and 1981. $l_x$ is the survivorship to age x, $b_x$ is the effective fecundity (see Appendix IV) at age x. The sum of their age-specific products, $\Sigma l_x b_x$, is the population replacement rate, $R_0$.

keep the population approximately stable over a longer period of time. The population may only be able to persist in this environment because of the occurrence of good emergence and/or seed production years.

Observed emergence in the transition zone in 1980 and 1981 was effectively constant. Seed rain in the two years was not. This suggests year to year variability in emergence rates. Seed rain in 1980 was low (Chapter 6) and therefore the emergence rate used in calculating $b_x$ may be unusually high.

Another factor contributing to the comparatively high $R_0$ in the transition zone may be the observed early reproduction. If the plants which flowered at Age 2 are hypothesized to flower a year later (feasible since there was no statistical difference between habitats in the numbers which flowered at Age 2; Chapter 5) the replacement rate drops to 1.81.

The presence of polycarpic individuals effects $l_x$ above Age 3, if polycarpic individuals flower at Age 3. The percentage of flowering plants in which polycarpy was observed was 0.045, 1% of the total population. By deleting 1% from Age 4 and Age 5 in the $l_x$ column, the replacement rate becomes 1.95. Assuming polycarpy at its highest observed level, 14.7% (a "good" year for polycarpy) the replacement rate rises to 2.13. Even at its highest rate the presence of polycarpy has only limited effect on the population rate of increase.

In the age-specific mortality models discussed in Chapter 1, it was predicted that as juvenile to seedling survivorship ratios (Hart 1977) or postflowering to juvenile survivorship ratios increased (Charnov and

Schaffer 1973), polycarpy would be favoured. In the slack, since the mortality risk increases with age ($C_2/C_1 < 1$), the slack would appear to be a more "annual" type habitat than the others (Table 7.3). Survivorship ratios in the dune ridge and transition zone fit Hart's (1977) description of a biennial habitat ($C_2 = C_1$). Postflowering survivorship relative to preflowering survival (P/C) suggests a more "perennial" type habitat in the transition zone, but the degree of polycarpy within populations makes this latter conclusion trivial. The life histories of co-occurring species within the habitats support these conclusions. If these populations were differentiating, we could expect a move towards polycarpy in the transition zone, and perhaps the same in the dune ridge, and monocarpy to become canalized in the slack populations.

The evidence presented here suggests that significant differentiation is not occurring, and that the expression of monocarpy and polycarpy is a plastic response. The potential for polycarpy exists in plants from all habitats, but is only expressed in a few plants in the transition zone, and it has minimal effect on the population rate of increase in this habitat. The obvious question is, why and how is polycarpy maintained in these populations? One explanation, and perhaps the most parsimonious one, may be found in the evolutionary history of the species. True polycarpy is the only (recorded) life history in the other subspecies of the species complex *campestris*, and also in the genus *Artemisia* (see Chapter 2). Perhaps the polycarpy observed at Pinery and in the greenhouse is a vestigial effect of a subspecies in transition towards obligate monocarpy, or a pleiotropic effect of no negative selection value.

| STAGE | | DUNE RIDGE | SLACK | TRANSITION ZONE |
|---|---|---|---|---|
| Seedling | $C_1$ | 0.49 | 0.27 | 0.48 |
| Juvenile | $C_2$ | 0.49 | 0.15 | 0.48 |
| Preflowering | C | 0.24 | 0.04 | 0.23 |
| Postflowering | P | 0.04 | 0 | 0.11 |
| | $C_2/C_1$ | 1.00 | 0.56 | 1.00 |
| | P/C | 0.07 | 0 | 0.24 |

Table 7.3 Survivorship to the end of the first year, $C_1$, from the beginning of the second year to flowering, $C_2$, total preflowering survival $C = C_1C_2$, and postflowering survival P, and survivorship ratios in the dune ridge, slack and transition zone.

Alternatively, the effect of facultative polycarpy on the rate of increase of an individual genotype, $R_g$, may be a more appropriate avenue to explore than population parameters (Hairston, Wilbur and Tinkle 1970), since natural selection operates on individuals within populations. A large number of plants have very low or zero fecundity. If polycarpy is a possibility, the plant may have a second chance to produce seed, and thus a possible positive fecundity. Its rate of increase would be potentially vastly increased. This is congruent with Smith-Gill's (1983) scheme of phenotypic modulation, with selection acting to modify the effects. The low or zero production of seeds is a passive response to the environment (Smith-Gill's phenotypic modulation). Selection may operate to minimize the effect by favouring individuals which can flower again. In the best of all possible situations, with high fecundity in both flowering events, the increase in $R_g$ would also be high, since the replacement rate would increase from $S^{1/3}$ to $(S^{1/3} + S^{1/5})$. Thus, given (1) that there are no adverse effects of carrying a gene for potential polycarpy, (2) a sufficient frequency of year-plant combinations when polycarpy is advantageous, and (3) gene flow between populations, facultative polycarpy may be maintained. If the potential for polycarpy is associated with indeterminate growth, then condition (1) is satisfied. Variation between years in the degree of polycarpy observed indicates that condition (2) may also be met. It is also likely that there is gene flow among the populations (see Chapter 6).

Sand dune systems are unique among successional series in that though the immediate habitat changes with time, all successional stages are continually being produced nearby, barring catastrophes (Watkinson,

Huiskes and Noble 1979). Short term changes are accompanied by long term predictability and accessibility. The ability to maintain sufficient plasticity to live successfully in habitats as diverse as the three studied here may be a better strategy than differentiation into populations with obligate life histories, and ensure the wide ecological amplitude viewed in this species at Pinery Provincial Park.

This study has helped to bridge the gap between empirical investigation and theoretical development of life history theory (Stearns 1976, 1977). It also helps to underline the naivete of much life history theory on which the study was based. It points out the necessity of incorporating plasticity in life history characters into theory, and cautions against assuming a genetically canalized optimal strategy without proper investigation of the genetics of the population studied. The complexity of the interaction between plants and their environment is also emphasized by the inability, at least in this study, to find a simple relationship between the habitats and the life history characters studied.

There are many questions left unanswered. Some of these questions are physiological and developmental, such as what factors control flowering and senescence in plants. Ecologically, the role of year to year variability between and within habitats needs further investigation. The importance of inflorescence structure and growth pattern (determinate or indeterminate) in the determination of obligate or facultative life histories may prove fruitful areas of future research. The presence of facultative life histories in other species and the controls on their expression are

necessary before we can understand the role of plasticity in this life history character.

# LIST OF APPENDICES

# APPENDIX I

## 1.1 Site description

All sites within a habitat type were numbered from 1 to 5, from the most southernwestern site to the most northeastern. The following comprises a brief subjective assessment of each site's vulnerability to disturbance, and any features which make a site obviously different from the main habitat type. The species lists (which follow Gleason 1963) were compiled in July 1981, and consist of only those species present within each plot. It is reported as the number of plots within a site which contain a given species. This is out of six plots unless otherwise indicated. Bare sand coverage was a subjective estimate determined by eye and is included only to provide a qualitative comparison between sites.

Appendix 1.2. Dune ridge

Site 1 was adjacent to Dunes Campground but disturbance from campers was minimal. Site 3 received pedestrian traffic from the main path into the Wilderness Area from the road. This disturbance appeared to increase over the period of the study. Site 5 was adjacent to the day-use area, but sufficiently removed from parking facilities so that human disturbance appeared minimal, though one plot in site 5 was irreplaceably vandalized in 1981. Thus species present is reported for only 5 plots in site 5. Range of bare sand coverage: Site 1 - 50-80%; 2 - 30-75%; 3 - 25-30%; 4 - 40-75%; 5 - 50-70%.

| Species present | Number of plots containing the species | | | | |
|---|---|---|---|---|---|
| | Site | | | | |
| | 1 | 2 | 3 | 4 | 5 |
| *Andropogon scoparius* Michx. | 5 | 2 | 4 | 4 | 1 |
| *Calamovilfa longifolia* (Hook.)Scribn. | 6 | 6 | 6 | 6 | 5 |
| *Corispermum hyssopifolium* L. | | 1 | 1 | 1 | 1 |
| *Lithospermum carolinense* (Walt.)Macmill. | | 1 | 2 | 1 | 1 |
| *Populus balsamifera* L. | 2 | 2 | | 1 | 2 |
| *Portulaca oleracea* L. | | | 1 | 2 | |
| *Prunus pumila* L. | 3 | 5 | 1 | | 1 |

Appendix 1.3. Slack

Site 1 was adjacent to DR1, and separated from the campground area by a transverse arm of the second dune ridge, which was approximately perpendicular to the shoreline. Sites 1 and 4 had the coarsest sand; site 2 had the finest. Sites 4 and 5, closest to the day-use area, suffered the greatest degree of vandalism. Two plots in site 4 were completely destroyed by (illegal) snowmobile use during the winter of 1979-80. Species present are thus reported for only 4 plots in this site. Stakes in two plots in site 5 were pulled out in 1980 but the plots were recoverable. Site 5 was the most disturbed of all the sites studied, due to its proximity to the day-use area and a moving dune. Range of bare sand coverage: Site 1 - 95-97%; 2 - 90-97%; 3 - 90-97%; 4 - 95-97%; 5 - 85-97%.

| Species present | Number of plots containing the species | | | | |
|---|---|---|---|---|---|
| | Site | | | | |
| | 1 | 2 | 3 | 4 | 5 |
| *Andropogon scoparius* Michx. | 2 | 5 | 2 | 2 | 5 |
| *Arenaria stricta* Michx. | | | | | 1 |
| *Calamovilfa longifolia* (Hook.)Scribn. | 5 | 6 | 6 | 4 | 5 |
| *Corispermum hyssopifolium* L. | 4 | 4 | 5 | 2 | 4 |
| *Equisetum vulgare* | | 1 | | | |
| *Lithospermum caroliniense* (Walt.)MacMill. | | | | | 1 |
| *Populus balsamifera* L. | 2 | | | | |
| *Prunus pumila* L. | 1 | | | | |
| *Smilacina stellata* (L.)Desf. | | 1 | | | |

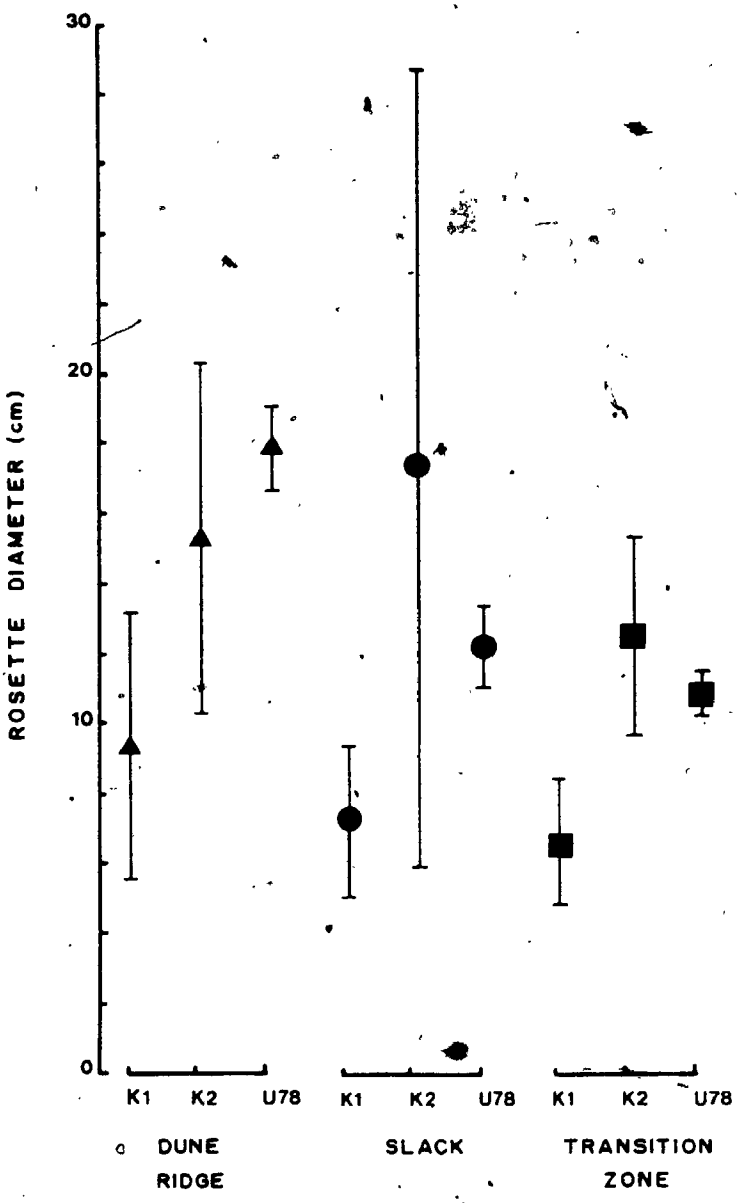
Appendix 1.4 Transition zone

Although the sites in the transition zone directly parallelled sites in other habitats, human disturbance was less here than in the other habitats. This was due to the presence of woody vegetation surrounding the sites, and to people's general proclivity to stay on already worn paths. Sites 3 and 4 were most subject to human disturbance. Sites 2 and 3 were adjacent to the second dune ridge, and site 2 in particular was occasionally subject to disturbance by sand movement. No plots were vandalized in any sites, perhaps because the posts were not easily seen in the surrounding vegetation, and they were harder to extract from the ground. Bare sand coverage: Site 1 - 5-30%; 2 - 5-50%; 3 - 5-75%; 4 - 5-75%; 5 - 5-50%.

| Species present | Number of plots containing the species | | | | |
|---|---|---|---|---|---|
| | Site | | | | |
| | 1 | 2 | 3 | 4 | 5 |
| *Andropogon gerardii* Vitm. | 1 | 1 | | | |
| *Andropogon scoparius* Michx. | 5 | 6 | 6 | 4 | 6 |
| *Arabis lyrata* L. | 2 | 1 | 2 | 2 | 4 |
| *Arctostaphylos uva-ursi* (L.)Spreng. | 6 | 6 | 6 | 4 | 5 |
| *Arenaria stellata* | 4 | 1 | 1 | 4 | 3 |
| *Calamovilfa longifolia* (Hook.)Scribn. | 6 | 6 | 6 | 4 | 5 |
| *Carex eburnea* Boott. | | | 1 | | 1 |
| *C. pensylvanicum* Lam. | 1 | 1 | 2 | | 3 |
| *C. umbellata* Schk. | 2 | | 2 | 3 | 2 |
| *Corispermum hyssopifolium* L. | | | 2 | | |
| *Fragaria virginiana* Duchesne | 1 | | | 3 | |
| *Koeleria cristata* (L.)Pers. | 1 | | 1 | | |
| *Liatris cylindracea* Michx. | 1 | | | 1 | 1 |
| *L. stricta* | 4 | 2 | 3 | 4 | 2 |
| *Lithospermum carolinense* (Walt.)MacMill. | | 2 | 1 | 1 | |
| *Pinus strobus* (L.) (seedling) | | 1 | | | |
| *Poa compressa* L. | 1 | | | | 2 |
| *Quercus spp.* (seedling) | | | 1 | 1 | |
| *Rosa blanda* Ait. | | | | 2 | 2 |
| *Senecio jacobaea* L. | | | 1 | | |
| *Smilacina stellata* (L.)Desf. | | 3 | 1 | 2 | |
| *Sorghastrum nutans* (L.)Nash. | 1 | 2 | 3 | 1 | 1 |
| *Stipa spartea* Trin. | 4 | | 2 | 3 | 3 |
| *Tortella tortuosa* | 6 | 5 | 6 | 4 | 5 |
| Lichen spp. | 2 | | 1 | | 3 |

# APPENDIX II

Appendix 2 Means and 95% confidence limits of rosette diameter from known age plants at Age 1 (K1) and Age 2 (K2) and plants tagged in 1978 (U78) in the dune ridge, slack and transition zone.


30
20
10
0
ROSETTE DIAMETER (cm)
K1
K2
U78
K1
K2
U78
K1
K2
U78
DUNE RIDGE
SLACK
TRANSITION ZONE

# APPENDIX III

## DESIGN VARIABLES

| HABITAT | H1 | H2 |
|---|---|---|
| DUNE RIDGE | -1 | -1 |
| SLACK | 0 | +1 |
| TRANSITION ZONE | +1 | 0 |

| AGE | A1 | A2 | A3 |
|---|---|---|---|
| 2 | -1 | -1 | -1 |
| 3 | 0 | 0 | +1 |
| 4 | 0 | +1 | 0 |
| 5 | +1 | 0 | 0 |

| DAMAGE | D1 |
|---|---|
| DAMAGE | -1 |
| NO DAMAGE | +1 |

Appendix 3 Design variables used in logistic regression analyses in Chapter 5. The first habitat variable, H1, calculates the effect of the transition zone habitat (valued + 1). H2 calculates the effect of the slack habitat. The effect of the dune ridge can be calculated as -(H1 + H2). Similarly, the first age variable, A1, refers to the effect of Age 5 (+ 1 in the table), the second to Age 4, etc. The damage variable, D1, is a simple contrast between damage and no damage.

# APPENDIX IV

## U.W.O. GREENHOUSE

| RESULTS | HABITAT OF ORIGIN | | | |
|---|---|---|---|---|
| | TZ | HB | SL | DR |
| Number successfully transplanted | 13 | 14 | 15 | 13 |
| Died midsummer 1980 | 0 | 3 | 1 | 0 |
| Attempted flowering 1980 | 2 | 1 | 4 | 2 |
| Died overwinter 1980-81 | 0 | 0 | 0 | 0 |
| Left alive May 1981 | 13 | 11 | 14 | 13 |
| Died juvenile midsummer 1981 | 1 | 0 | 0 | 0 |
| Attempted flowering 1981 | 2 | 4 | 5 | 4 |
| Died flowering 1981 | 0 | 1 | 0 | 0 |
| Died juvenile overwinter 1981-82 | 0 | 0 | 0 | 0 |
| Died flowering overwinter 1981-82 | 0 | 0 | 0 | 0 |
| Entered 1982 juvenile | 8 | 6 | 5 | 7 |
| Attempted flowering 1982 | 1 | 2 | 2 | 1 |
| Died flowering 1982 | 0 | 0 | 0 | 0 |
| Died juvenile 1982 | 0 | 1 | 2 | 3 |
| Survived juvenile 1982 | 7 | 3 | 1 | 2 |

Appendix 4.1 Fate of plants (in numbers) grown in the U.W.O. greenhouse as part of the reciprocal transplant-replant experiment. TZ = transition zone; HB = high beach; SL = slack; DR = dune ridge.

LABATT FIELD STATION

| RESULTS | HABITAT OF ORIGIN | | | |
|---|---|---|---|---|
| | TZ | HB | SL | DR |
| Number successfully transplanted | 13 | 14 | 15 | 13 |
| Died midsummer 1980 | 0 | 0 | 0 | 0 |
| Attempted flowering 1980 | 0 | 1 | 1 | 1 |
| Died overwinter 1980-81 | 8 | 7 | 5 | 3 |
| Left alive May 1981 | 5 | 7 | 10 | 10 |
| Died juvenile midsummer 1981 | 0 | 0 | 1 | 1 |
| Attempted flowering 1981 | 5 | 7 | 9 | 9 |
| Died flowering 1981 | 0 | 1 | 1 | 0 |
| Died juvenile overwinter 1981-82 | 0 | 0 | 0 | |
| Died flowering overwinter 1981-82 | 5 | 6 | 8 | 9 |

Appendix 4.2 Fate of plants (in numbers) grown at Labatt Field Station in the reciprocal transplant-replant experiment. TZ = transition zone; HB = high beach; SL = slack; DR = dune ridge.

PINERY PROVINCIAL PARK

| HABITAT OF ORIGIN: | TRANSITION ZONE | | HIGH BEACH | |
|---|---|---|---|---|
| EXPERIMENTAL LOCATION: | TZ | HB | TZ | HB |
| Number successfully transplanted | 13 | 13 | 14 | 14 |
| Died midsummer 1980 | 1 | 1 | 1 | 0 |
| Attempted flowering 1980 | 0 | 0 | 0 | 0 |
| Died overwinter 1980-81 | 2 | 11 | 3 | 11 |
| Left alive May 1981 | 10 | 1 | 10 | 3 |
| Died juvenile midsummer 1981 | 0 | 0 | 2 | 0 |
| Attempted flowering 1981 | 8 | 1 | 6 | 3 |
| Died flowering 1981 | 0 | 0 | 0 | 0 |
| Died juvenile overwinter 1981-82 | 0 | 0 | 0 | 0 |
| Died flowering overwinter 1981-82 | 4 | 1 | 3 | 1 |
| Entered 1982 juvenile | 2 | 0 | 2 | 0 |
| Attempted flowering 1982 | 1 | | 2 | |
| Died flowering 1982 | 0 | | 0 | |
| Died juvenile 1982 | 0 | | 0 | |
| Survived juvenile 1982 | 0 | | 0 | |

Appendix 4.3 Fate of plants (in numbers) grown at Pinery Provincial Park in the reciprocal transplant-replant experiment. TZ = transition zone; HB = high beach.

# APPENDIX V

| HABITAT | AGE | $p(f_x)$ | $p(f)_s$ | b | e | $b_x$ |
|---|---|---|---|---|---|---|
| DUNE RIDGE | 1 | 0 | | | | |
| | 2 | 0 | | | | |
| | 3 | 0.65 | 0.88 | 240 | 0.025 | 3.432 |
| | 4 | 0.40 | 0.88 | 240 | 0.025 | 2.112 |
| | 5 | 0.33 | 0.88 | 240 | 0.025 | 1.742 |
| SLACK | 1 | 0 | | | | |
| | 2 | 0 | | | | |
| | 3 | 0.48 | 0.73 | 500 | 0.134 | 23.477 |
| | 4 | 0.54 | 0.73 | 500 | 0.134 | 26.411 |
| | 5 | 0.50 | 0.73 | 500 | 0.134 | 24.455 |
| TRANSITION ZONE | 1 | 0 | | | | |
| | 2 | 0.14 | 0.74 | 120 | 0.096 | 1.193 |
| | 3 | 0.38 | 0.74 | 120 | 0.096 | 3.239 |
| | 4 | 0.34 | 0.74 | 120 | 0.096 | 2.898 |
| | 5 | 0.35 | 0.74 | 120 | 0.096 | 2.984 |

Appendix 5 Calculation of effective fecundity $b_x$ at each age within habitats. $b_x$ was estimated as the product of the probability of flowering at age x ($p(f_x)$), the probability of successful flowering $p(f_s)$, the geometric mean of seed production (b) and the emergence rate of seeds (e).

# REFERENCES


Alexander, H. M., and R. D. Wulff (1985). Experimental ecological genetics in *Plantago*. X. The effects of maternal temperature on seed and seedling characters in *P. lanceolata*. J. Ecol. 73: 271-82.

Angevine, Mark and Brian F. Chabot (1979). Seed germination syndromes in higher plants. In Topics in Plant Population Biology. O. T. Solbrig, S. Jain, G. B. Johnson and P. H. Raven (eds). Columbia University Press, New York.

Antonovics, Janis (1968). Evolution in closely adjacent populations. VI. Manifold effects of gene flow. Heredity 23: 507-24.

Arthur, A. E., J. S. Gale and M. J. Lawrence (1973). Variation in wild populations of *Papaver dubium*. VII. Germination time. Heredity 30: 189-97.

Augspurger, Carol K. (1981). Reproductive synchrony of a tropical shrub: experimental studies on effects of pollinators and seed predators on *Hybanthus prunifolius* (Violaceae). Ecology 62: 775-88.

Baldwin, K. A. (1982). Comparative microenvironmental studies in some primary sand dune habitats at Pinery Provincial Park, Ontario. MSc thesis. University of Western Ontario, London, Ontario.

Baldwin, K. A. and M. A. Maun (1983). Microenvironment of Lake Huron sand dunes. Can. J. Bot. 61: 241-55.

Baskin, J. M. and C. C. Baskin (1979a). Studies in the autecology and population biolgy of the monocarpic perennial *Grindelia lanceolata*. Am. Midl. Nat. 102: 290-99.

Baskin, J. M. and C. C. Baskin (1979b). Studies in the autecology and population biology of the weedy monocarpic perennial *Festuca sativa*. J. Ecol. 67: 601-10.

Bell, Graham (1976). On breeding more than once. Amer. Natur. 110: 57-77.

Bell, Graham (1980). The costs of reproduction and their consequences. Amer. Natur. 116: 45-76.

Bentley, S., J. B. Whittaker and A. J. C. Malloch (1980). Field germination experiments on the effects of grazing by a chrysomelid beetle (*Gastrophysa viridula*) on seed production and quality in *Rumex obtusifolius* and *Rumex crispus*. J. Ecol. 68: 671-74.

Bishop, Y., S. Fienberg and P. Holland (1975). Discrete Multivariate Analysis. Theory and Practice. M.I.T. Press, Cambridge, Massachusetts.

Boorman, L. A. (1982). Some plant growth patterns in relation to the sand dune habitat. J. Ecol. 70: 607-14.

Bowles, J. M. (1980). Effects of human disturbance on dunes at Pinery Provincial Park. PhD thesis, University of Western Ontario, London, Ontario.

Bradshaw, A. D. (1965). Evolutionary significance of phenotypic plasticity in plants. Adv. Genet. 13: 115-55.

Bradshaw, A.D. (1972). Some of the evolutionary consequences of being a plant. Evol. Biol. 5:25-47.

Bradshaw, A.D. (1984). Ecological significance of genetic variation between populations. In Perspectives on Plant Population Ecology. Rodolfo Dirzo and Jose Sarukhan (eds). Sinauer Associates Inc., Sunderland, Massachusetts.

Breslow, N. (1970). A generalized Kruskal-Wallis test for comparing k samples subject to unequal patterns of censorship. Biometrika 57: 579-94.

Cameron, Ewen (1935). A study of the natural control of ragwort (*Senecio jacobaea* L.). J. Ecol. 23: 266-322.

Caswell, Hal (1983). Phenotypic plasticity in life-history traits: demographic effects and evolutionary consequences. Amer. Zool. 23: 35-46.

Caswell, Hal and P.A. Werner (1978). Transient behaviour and life history analysis of teasel (*Dipsacus sylvestris* Huds.). Ecology 59: 53-66.

Charnov, Eric L. and William M. Schaffer (1973). Life historical consequences of natural selection: Cole's result revisited. Amer. Natur. 107: 791-93.

Cole, L. C. (1954). The population consequences of life history phenomena. Quart. Rev. Biol. 29: 103-37.

Cook, Robert Edward (1980). Germination and size dependent mortality in *Viola blanda*. Oecologia (Berlin) 47: 115-17.

Crawley, Michael J. (1983). Herbivory: The Dynamics of Animal-Plant Interactions. Studies in Ecology Vol. 10. University of California Press. Berkeley and Los Angeles.

Dawson, Peter S. and Russell A. Riddle (1983). In Population Biology: Prospect and Retrospect. Charles E. King and Peter S. Dawson (eds). Columbia University Press, New York.

Deevey, E. S. (1947). Life tables for natural populations of animals. Quart. Rev. Biol. 22: 283-314.

Dixon, W. J. (1983). BMDP-83 Biomedical Computer Programs, P-Series. University of California Press, Berkeley.

Dirzo, Rodolfo and Jose Sarukhan (eds) (1984). Perspectives on Plant Population Ecology. Sinauer Associates Inc., Sunderland, Massachusetts.

Elliott, J. M. (1977). Some Methods for the Statistical Analysis of Samples of Benthic Invertebrates. Freshwater Biological Association Scientific Publication No. 25.

Faegri, K. and L. van der Pijl (1979). The Principles of Pollination Ecology (3rd edition). Pergamon Press, New York.

Fenner, M. (1978). A comparison of the abilities of colonizers and closed turf species to establish from seed in artificial sward. J. Ecol. 66: 953-63.

Ford, E.D. (1975). Competition and stand structure in some even-aged plant monocultures. J. Ecol. 63: 611-33.

Fowler, N. L. (1984). The role of germination date, spatial arrangement and neighbourhood effects in competitive interactions in *Linum*. J. Ecol. 72: 307-18.

Fowler, Norma and Janis Antonovics (1981). Small scale variability in the demography of transplants of two herbaceous species. Ecology 62: 1450-57.

Friedman, Jacob and Gideon Orshan (1975). The distribution, emergence and survival of seedlings of *Artemisia herba-alba* asso. in the Negev Desert of Israel in relation to distance from adult plant. J. Ecol. 63: 627-32.

Gadgil, Madhav and Otto T. Solbrig (1972). The concept of r and K selection: evidence from wildflowers and some theoretical considerations. Amer. Natur. 106: 14-31.

Gleason, H.A. and A. Cronquist (1963). Manual of Vascular Plants of Northeastern United States and Adjacent Canada. D. van Nostrand Co. Inc., Princeton, New Jersey.

Grime, J.P. (1977). Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Amer. Natur. 111: 1169-84.

Grime, J. P. and R. Hunt (1975). Relative growth rate: its range and adaptive value in a local flora. J. Ecol. 63: 393-422.

Gross, Katherine Lynn (1980). Ecological consequences of differences in life history characteristics among four "biennial" plant species. PhD thesis, Michigan State University, East Lansing, Michigan.

Gross, K.L. (1981). Predictions of fate from rosette size in four "biennial" plant species: *Verbascum thapsus, Oenothera biennis, Daucus carota* and *Tragopogon dubius*. Oecologia (Berlin) 48: 209-13.

Gross, Katherine L. (1984). Effects of seed size and growth form on seedling establishment of six monocarpic perennial plants. J. Ecol. 72: 369-387.

Gross, R. S. and P. A. Werner (1983). Probabilities of survival and reproduction relative to rosette size in the common burdock (*Arctium minus*: Compositae). Am. Midl. Nat. 109: 184-93.

Gutterman, Y. (1973). Differences in the progeny due to daylength and hormone treatment of the mother plant. In Seed Ecology. W. Heydecker (ed). Butterworths, London.

Hairston, Nelson G., Donald W. Tinkle and Henry M. Wilbur (1970). Natural selection and the parameters of population growth. J. Wildl. Mgmt. 34: 681-90.

Hall, Harvey M. and Frederic E. Clements (1923). The Phylogenetic Method in Taxonomy: The North American Species of *Artemisia, Chrysothamnus* and *Atriplex*. Carnegie Institute of Washington.

Hamrick, J. L. (1982). Plant population genetics and evolution. Amer. J. Bot. 69: 1685-93.

Harper, J. L. (1967). A Darwinian approach to plant ecology. J. Ecol. 55: 247-70.

Harper, John L. (1977). Population Biology of Plants. Academic Press, London, New York and San Francisco.

Harper, J. L., P. H. Lovell and K. G. Moore (1970). The shapes and sizes of seeds. Ann. Rev. Ecol. Syst. 1: 327-56.

Harper, J. L. and John Ogden (1970). The reproductive strategy of higher plants. I. The concept of strategy with special reference to *Senecio vulgaris* L. J. Ecol. 58: 681-98.

Harper, J.L., J.T. Williams and G.R. Sagar (1965). The behaviour of seeds in the soil. Part I. The heterogeneity of soil surfaces and its role in determining the establishment of plants from seeds. J. Ecol. 63: 273-86.

Hart, R. (1977). Why are biennials so few? Amer. Natur. 1f1: 792-99.

Hartgerink, A. P. and F. A. Bazzazz (1984). Seedling scale environmental heterogeneity influences individual fitness and population structure. Ecology 65: 198-206.

Hartnett, David C. and Warren G. Abrahamson (1979). The effects of stem gall insects on life history patterns in *Solidago canadensis*. Ecology 60: 910-17.

Hastings, Alan and Hal Caswell (1979). Role of environmental variability in the evolution of life history strategies. Proc. Natl. Acad. Sci. U.S.A. 76: 4700-03.

Hawthorn, Wayne R. and Paul B. Cavers (1976). Population dynamics of the perennial herbs *Plantago major* L. and *P. rugelii* Decne. J. Ecol. 64: 511-27.

Heslop-Harrison, J. (1965). Reflections on the role of reproductive versatility in the adaptation of plant populations. Trans. and Proc. Bot. Soc. Edinburgh 40: 159-69.

Hett, Joan M. (1971). A dynamic analysis of age in sugar maple seedlings. Ecology 52: 1071-4.

Heywood, V. H. and C. J. Humphries (1977). Anthemidae - systematic review. In The Biology and Chemistry of the Compositae Vol. II. V. H. Heywood, J. B. Harborne and B. L. Turner (eds). Academic Press, London, New York and San Francisco.

Hickman, James C. (1975). Environmental unpredictability and plastic energy allocation strategies in the annual *Polygonum cascadense* (Polygonaceae). J. Ecol. 63: 689-701.

Hicks, Mary Louise (1938). The growth of *Artemisia caudata* Michx. in relation to certain environmental conditions, particularly nitrogen supply and light intensity. MSc. thesis, University of Chicago, Chicago, Illinois.

Hirose, T. and N. Kachi (1982). Critical plant size for flowering in biennials with special reference to their distribution in a sand dune system. Oecologia (Berlin) 55: 281-84.

Holt, Buford R. (1972). Effect of arrival time on recruitment, mortality and reproduction in successional plant populations. Ecology 53: 668-73.

Howell, Nicholas (1981). The effect of seed size and relative emergence time on fitness in a natural population of *Impatiens capensis* Meerb. (Balsaminaceae). Am. Midl. Nat. 105: 312-320.

Hume, L. and P. B. Cavers (1981). A methodological problem in genecology. Seeds vs. clones as source material for uniform gardens. Can J. Bot. 59: 763-68.

Jain, Subodh (1979). Adaptive strategies: polymorphism, plasticity and homeostasis. In Topics in Plant Population Biology. O.T. Solbrig, S. Jain, G.B. Johnson and P.H. Raven (eds). Columbia University Press, New York.

Jain, S.K. and A.D. Bradshaw (1966). Evolutionary divergence among adjacent plant populations. I. The evidence and its theoretical analysis. Heredity 21: 407-41.

Jefferies, R. L., A. J. Davy and T. Rudmick (1981). Population biology of the salt marsh annual *Salicarnia europaea* agg. J. Ecol. 69: 17-31.

Johnson, M. P. and S. A. Cook (1968). "Clutch size" in buttercups. Amer. Natur. 102: 405-411.

Johnson, Christine D. and A. G. Thomas (1978). Recruitment and survival of seedlings of a perennial *Hieracium* species in a patchy environment. Can. J. Bot. 56: 572-80.

Kaplan, E. L. and P. Meier (1958). Nonparametric estimation from incomplete observations. J. Amer. Statist. Assoc. 53: 457-481.

Keddy, P. A. (1981). Experimental demography of the sand dune annual *Cakile edentula*, growing along an environmental gradient in Nova Scotia. J. Ecol. 69: 615-30.

Kelly, David (1985a). Why are biennials so maligned? Amer. Natur. 125: 473-79.

Kelly, David (1985b). On strict and facultative biennials. Oecologia (Berlin) 67: 292-94.

Kershaw, K.A. (1973). Quantitative and dynamic plant ecology. 2nd edition. Edward Arnold, London.

Kiang, Y.T. and J.L. Hamrick (1978). Reproductive isolation in the *Mimulus guttatus-M. nasutus* complex. Am. Midl. Nat. 100: 269-76.

King, Charles and Peter S. Dawson (eds) (1983). Population Biology: Prospect and Retrospect. Columbia University Press, New York.

Klemow, Kenneth M. and Dudley J. Raynal (1981). Population ecology of *Melilotus alba* in a limestone quarry. J. Ecol. 69: 33-44.

Law, R. (1979). The costs of reproduction in annual meadow grass. Amer. Natur. 113: 3-16.

Law, R. (1981). Ecological determinants in the evolution of life histories. In Population Dynamics. R. M. Anderson, B. D. Turne and L. R. Taylor (eds). Blackwell Scientific Publications, London.

Lawless, J. F. (1982). Statistical Models and Methods for Lifetime Data. John Wiley and Sons; Toronto.

Lee, Janet M. and J.L. Hamrick (1983). Demography of two natural populations of musk thistle (*Carduus nutans*). J. Ecol. 71: 923-36.

Leverich, W. J. and D. A. Levin (1979). Age specific survivorship and fecundity in *Phlox drummondii* Hook. Amer. Natur. 113: 881-903.

Levin, Donald A. (1983). Plant parentage: an alternate view of the breeding structure of populations. In Population Biology: Prospect and Retrospect. Charles E. King and Peter S. Dawson (eds). Columbia University Press, New York.

Levin, D. A. and H. W. Kerster (1974). Gene flow in seed plants. Evol. Biol. 7: 139-220.

Levins, Richard (1968). Evolution in Changing Environments. Princeton University Press, Princeton, New Jersey.

MacArthur, R.H. and E.O. Wilson (1967). The Theory of Island Biogeography. Princeton University Press, Princeton, New Jersey.

Mantel, N. (1966). Evaluation of survival data and two new rank order statistics arising in its consideration. Cancer Chemotherapy Reports 50: 163-70.

Marks, M. and S. Prince (1981). Influence of germination date on survival and fecundity in wild lettuce *Lactuca serriola*. Oikos 36: 326-30.

Marshall, D. L., D. A. Levin and N.L. Fowler (1985). Plasticity in yield components in response to fruit predation and date of fruit initiation in three species of *Setobania* (Leguminoseae). J. Ecol. 73: 71-81.

Maruta, Emiko (1976). Seedling establishment of *Polygonum cuspidatum* on Mount Fuji. Jap. J. Ecol. 26: 101-5.

Maun, M. A. (1974). Viability of *Rumex crispus* seeds harvested at different stages of maturity. Can. J. Plant Sci. 54: 547-52.

Maun, M. A. (1981). Seed germination and seedling establishment of *Calamovilfa longifolia* on Lake Huron sand dunes. Can J. Bot. 59: 460-69.

Maun, M. A. and P. B. Cavers (1971). Seed production and dormancy in *Rumex crispus*. I. The effects of removal of cauline leaves at anthesis. Can. J. Bot. 49: 1123-30.

Mayr, Ernst (1963). Animal Species and Evolution. Harvard University Press, Cambridge, Massachusetts.

McNeilly, T. (1968). Evolution in closely adjacent populations. III. *Agrostis tenuis* on a small copper mine. Heredity 23: 99-108.

McNeilly, Thomas and Janis Antonovics (1967). Evolution in closely adjacent plant populations. IV. Barriers to gene flow. Heredity 23: 205-218.

Mead, R. (1966). A relationship between individual plant spacing and yield. Ann. Bot. 30: 301-9.

Mithen, Richard, John L. Harper and Jacob Weiner (1984). Growth and mortality of individual plants as a function of "available area". Oecologia (Berlin) 62: 57-60.

Morrison, R. G. (1973). Primary sand dune succession at Grand Bend, Ontario. PhD thesis, University of Toronto, Toronto, Ontario.

Morrison, R. G. and G. A. Yarranton (1974). Diversity, richness and evenness during a primary sand dune succession at Grand Bend, Ontario. Can. J. Bot. 51: 2401-11.

Murphy, Garth I. (1968). Pattern in life history and the environment. Amer. Natur. 102: 391-402.

Newell, Sandra J., Otto T. Solbrig and Dwight T. Kincaid (1981). Studies in the population biology of the genus *Viola*. III. The demography of *Viola blanda* and *V. pallens*. J. Ecol. 69: 997-1016.

Obeid, M., D. Machin and John L. Harper (1967). Influence of density on plant to plant variation in fiber flax *Linum usitatissimum* L. Crop Science 7: 471-73.

Olson, J. S. (1958a). Rates of succession and soil changes in southern Lake Michigan sand dunes. Bot. Gaz. 119: 125-70.

Palmblad, I. G. (1968). Comparative response of closely related species to reduced competition. I. *Senecio sylvaticus* and *S. viscosus*. Can. J. Bot.

46: 225-28.

Pemadasa, M. A. and P. H. Lovell (1974). Factors affecting the distribution of some annuals in the dune system at Aberffraw, Anglesey. J. Ecol. 62: 403-16.

Pianka, Eric R. (1972). r and K selection or b and d selection? Amer. Natur. 106: 581-88.

Pielou, E. C. (1977). Mathematical Ecology. Wiley, New York.

Primack, Richard B. (1978). Evolutionary aspects of wind pollination in the genus *Plantago* (Plantaginaceae). New Phytol. 81: 449-58.

Quinn, J. A. and J. C. Colosi (1977). Separating ecotype from environment in germination ecology studies. Am. Midl. Nat. 97: 484-89.

Rabinowitz, Deborah (1979). Bimodal distributions of seedling weight in relation to density of *Festuca paradoxa* Desv. Nature 277: 297-98.

Ritland, Kermit and Subodh Jain (1984). A comparative study of floral and electrophoretic variation with life history variation in *Limnanthes alba* (Limnanthaceae). Oecologia (Berlin) 63: 243-51.

Rowe, Stan J. (1964). Environmental preconditioning, with special reference to forestry. Ecology 45: 399-403.

Ross, M. A. and John L. Harper (1972). Occupation of biological space during seedling establishment. J. Ecol. 60: 77-88.

Ryan, T. A., B. L. Jourier and B. F. Ryan (1978). Minitab II Reference Manual. Duxbury Press, Massachusetts.

Sachs, R. M. and W. P. Hackett (1983). Source-sink relationships and flowering. In Strategies of Plant Reproduction. Beltsville Symposia in Agricultural Research Vol. 6. Werner J. Meudt (ed). Allanheld, Osmun Publishers, Totowa, New Jersey.

Salisbury, Edward (1975). The survival modes of dispersal. Proc. R. Soc. Lond. B 188: 183-88.

Sarukhan, Jose and John L. Harper (1973). Studies in plant demography: *Ranunculus repens* L., *R. bulbosus* L. and *R. acris* L. I. Population flux and survivorship. J. Ecol. 61: 675-716.

Schaal, Barbara A. (1980). Reproductive capacity and seed size in *Lupinus texensis*. Amer. J. Bot. 67: 703-9.

Schaal, Barbara A. (1984). Life history variation, natural selection and maternal effects in plant populations. In Perspectives on Plant Population Ecology. Rodolfo Dirzo and Jose Sarukhan (eds). Sinauer Associates Inc. Sunderland, Massachusetts.

Schaffer, William M. and Madhav Gadgil (1975). Selection for optimal life histories in plants. In Ecology and Evolution of Communities. M. L. Cody and J. M. Diamond (eds). Belknap Press, Cambridge, Massachusetts and London, England.

Schemske, Douglas W. (1977). Flowering phenology and seed set in *Claytonia virginica* (Portulacaceae). Bull. Torr. Bot. Club 104: 254-63.

Scoggan, H.J. (1979). The Flora of Canada Part 4 - Dicotyledonae. National Museum of Natural Sciences Publication No. 7(4). National Museums of Canada.

Silvertown, Jonathan W. (1982). Introduction to Plant Population Ecology. Longman, London and New York.

Silvertown, Jonathan W. (1983). Why are biennials sometimes not so few? Amer. Natur. 121: 448-453.

Smith, H. (1973). Light quality and germination: ecological implications. In Seed Ecology. W. Heydecker (ed). Butterworths, London.

Smith-Gill, Sandra J. (1983). Developmental plasticity vs. phenotypic modulation. Amer. Zool. 23: 47-55.

Snaydon, R.W. and M.S. Davies (1972). Rapid population differentiation in a mosaic environment. II. Morphological variation in *Anthoxanthum odoratum*. Evolution 26: 390-405.

Snaydon, R.W. and M.S. Davies (1976). Rapid population differentiation in a mosaic environment. IV. Populations of *Anthoxanthum odoratum* at sharp boundaries. Heredity 37: 9-25.

Snedecor, George W. and William G. Cochran (1980). Statistical Methods. 7th edition. Iowa State University Press, Ames, Iowa.

Sokal, Robert R. and F. James Rohlf (1969). Biometry. W.H. Freeman Co., San Francisco.

Sokal, Robert R. and F. James Rohlf (1981). Biometry. 2nd. edition. W.H. Freeman Co., San Francisco.

Solbrig, Otto T. (1981). Studies in the population biology of the genus *Viola*. II. The effect of plant size on fitness. Evolution 35: 1080-93.

Solbrig, O.T., Sandra J. Newell and D. T. Kincaid (1980). The population biology of the genus *Viola*. I. The demography of *Viola sorania*. J. Ecol. 68: 521-46.

Stearns, Forest (1960). Effects of seed environment during maturation on seedling growth. Ecology 41: 221-22.

Stearns, S. C. (1976). Life history tactics: a review of the ideas. Quart. Rev. Biol. 51: 3-47.

Stearns, S. C. (1977). The evolution of life history traits. Ann. Rev. Ecol. Syst. 8: 145-71.

Stearns, S.C. (1980). A new view of life history evolution. Oikos 35: 266-81.

Stebbins, G. L. (1950). Variation and Evolution in Plants. Columbia University Press, New York.

Sterk, A.A. (1975). Demographic studies of *Anthyllis vulneraria* L. in the Netherlands. Acta. Bot. Neerl. 24: 315-37.

Thompson, John N. (1983). Partitioning of variance in demography: within patch differences in herbivory, survival and flowering of *Lomatium farinosum* (Umbelliferae). Oikos 40: 315-17.

Thompson, K. (1984). Why biennials are not as few as they ought to be. Amer. Natur. 123: 854-61.

Thompson, P.A. (1973). Geographical adaptation of seeds. In Seed Ecology. W. Heydecker (ed). Butterworths, London.

Tremlett, Mark, Jonathan W. Silvertown and Aris Tucker (1984). An analysis of spatial and temporal variation in seedling survival of a monocarpic perennial *Conium maculatum*. Oikos 43: 41-45.

Van der Meijden, E. and R. E. van der Waals-Kooi (1979). The population ecology of *Senecio jacobaea* in a sand dune system. I.Reproductive strategy and the biennial habit. J. Ecol. 67: 131-53.

Walker, S. H. and D. B. Duncan (1967). Estimation of the probability of an event as a function of several different variables. Biometrika 54: 167-79.

Watkinson, A. R., A. H. L. Huiskes and J. C. Noble (1979). The demography of sand dune species with contrasting life cycles. In Ecological Processes in Coastal Environments. R.L. Jefferies and A.J. Davy (eds). Blackwell Scientific Publications, Oxford.

Weaver, Susan E. and Paul B. Cavers (1979). The effects of date of emergence and emergence order on seedling survival rates in *Rumex crispus* and

*Rumex obtusifolius*. Can. J. Bot. 57: 730-38.

Weiner, Jacob and Otto T. Solbrig (1984). The meaning and measurement of size hierarchies in plant populations. Oecologia (Berlin) 61: 334-36.

Werner, P. A. (1975). Predictions of fate from rosette size in teasel (*Dipsacus fullonum*). Oecologia (Berlin) 20: 197-201.

Werner, P. A. (1977). Colonization success of a "biennial" plant species. experimental field studies of species cohabitation and replacement. Ecology 58: 840-49.

Werner, P. A. and H. Caswell (1977). Population growth rates and age versus stage distribution models for Teasel (*Dipsacus fullonum* Huds.). Ecology 58: 1103-11.

White, J. and J. L. Harper (1970). Correlated changes in plant size and number in plant populations. J. Ecol. 58: 467-85.

Whitehead, Donald R. (1969). Wind pollination in the angiosperms: evolutionary and environmental considerations. Evolution 23: 28-35.

Wilbur, Henry M. (1976). Life history evolution in seven milkweeds of the genus *Asclepias*. J. Ecol. 64: 223-40.

Woolhouse, Harold W. (1983). Hormonal control of senescence allied to reproduction in plants. In. Strategies of Plant Reproduction. BARC Symposia No. 6. Werner J. Meudt (ed). Allanheld, Osmun Publishers. Totowa, New Jersey.

Young, Truman P. (1981). A general model of comparative fecundity for semelparous and iteroparous life histories. Amer. Natur. 118: 27-36.

# END

# 08 04 87

# FIN